• A NEW SERIES OF PLANT SCIENCE BOOKS •

edited by Frans Verdoorn

Volume VII

A SHORT HISTORY *of* THE PLANT SCIENCES

BY THE SAME AUTHOR:-

Brief history of ecological work in botany. Plant World 8:163, 198. 1905.

Stimulation of plant growth by weak poisons. BAILEY's Encyclopedia of Agriculture. II: 1907.

Value of certain nutritive elements to the plant cell. Annals of Botany 20:501. 1907.

Modern and early ideas upon the subject of root excretions. Popular Science Monthly 73:257. 1908.

Manual of bacteriology for agricultural and general science students. Boston, New York (etc.). Ginn and Co. 1914.

Cedar rust disease of apples caused by Gymnosporangium juniperi-virginianae. Va. Agr. Exp. Sta. Tech. Bull. 9. 1915. (With C. H. CRABILL).

Nature of the growth rate. Jour. Gen. Phys. 2:545-561. 1920.

Growth and sap concentration. Jour. Agr. Res. 21:81-98. 1921.

What can biology contribute to the world of today? 1923, Riverside, California.

Quantitative aspects of the problem of growth and differentiation. International Congress of Plant Science, Ithaca, New York. Proceedings, 2:1095-1106. 1929.

Random observations on citrus fruits abroad. California Citrograph 16. Nov. 1930.

La nature de la croissance. Bull. Soc. Botanique Génève 24:202-219. 1931-32.

The effects of zinc and iron salts on the cell structure of mottled orange leaves. Hilgardia 9:113-139. Jan. 1935. (With J. DUFRÉNOY).

Cellular nutrition and immunity. Rapports du 3e Congrès Internationale de Pathologie comparée. Athens, 1936.

Ixtlilxochitl II and Cempoallan: a preliminary study of a Mexican Picture Chronicle. Hispanic American Historical Review 18:66-75. 1938.

Cytology of leaves affected with little-leaf. American Journal of Botany 25: 174-186. 1938.

HOWARD SPRAGUE REED was born, August 6, 1876, at North East, Pennsylvania. A.B., University of Michigan, 1903; Ph.D., University of Missouri, 1907. Pursued investigations at Naples Zoological Station (Smithsonian Inst. table), 1913; Strassburg, 1913; Geneva, 1930. Asst. in plant physiology, Univ. Michigan, 1899-1903; Instructor in botany, Univ. Missouri, 1903-06; Soil chemist, Bureau of Soils, U. S. Dept. Agr., 1906-1908; Prof. mycology and bacteriology, Virginia Polytechnic Inst. and plant pathologist in Expt. Sta., 1908-15; Professor plant physiology, Univ. of California, Citrus Expt. Sta., 1915-35; Univ. 1935—. Guest prof. Geneva, 1930; External exam. Sydney, 1935. Member edit. bd. of *Growth;* Assoc. Edit. of Univ. California Publ. Agr. Sci., 1922-35. Bronze Medal, Soc. Nat. d'Acclimat. de France, 1935; Correspondant du Mus. d'Histoire Nat. de Paris.

A SHORT HISTORY

of the

PLANT SCIENCES

BY

HOWARD S. REED

Professor of Plant Physiology

University of California

1942

WALTHAM, MASS., U.S.A.

Published by the Chronica Botanica Company

First published MCMXLII
By the Chronica Botanica Company
of Waltham, Mass., U. S. A.

New York, N. Y.: G. E. Stechert and Co.,
31 East 10th Street.

San Francisco, Cal.: J. W. Stacey, Inc.,
236-238 Flood Building.

Toronto 2.: Wm. Dawson, Ltd.,
70 King St., East.

Buenos Aires: Acme Agency,
Diagonal Norte 567.

Rio de Janeiro: Livraria Kosmos,
Caixa Postal 3481.

London W. 1.: Wm. Dawson & Sons, Ltd.,
83a Marylebone High Street.

Moscow: Mezhdunarodnaja Kniga,
Kusnetzki Most 18.

Tokyo: Maruzen Company, Ltd.,
6 Nihonbashi; P. O. Box 605.

Calcutta: Macmillan and Co., Ltd.,
294, Bow Bazar Street.

Johannesburg, S. A.: Juta and Company, Ltd.,
43, Gritchard Street.

Sydney: Angus and Robertson, Ltd.,
89 Castlereagh Street.

Made and printed in the U. S. A.

INTRODUCTION

Work on the history of a subject is inevitably a reflection of the interest of the writer. This is especially true in writing a book which deals with historical matters. I am not only aware of many great omissions in the writing of this book, but also of my own inability to treat certain of the subjects. I have preferred to deal with subjects on which I felt some competency, rather than to cover a large number of subjects so briefly that the account would scarcely be readable. I will take this opportunity to note that there has been adequate treatment in various recent books of subjects such as systematic botany, phylogeny, and paleobotany, to which the reader may go. The new field of genetics, with its cosmic subject of plant breeding and evolution, has been discussed recently by several competent writers. In similar fashion, the new work on growth, tropisms, and hormones has been discussed by WENT, THIMANN, and others. I have discussed the subject of plant geography to the end of the nineteenth century, preferring to refrain from discussion of recent work in ecology, sociology, etc., in which it seems that the concepts are so lacking in precise definition that discussion of them can wait for the pen of another writer.

The account of work in the plant sciences given in this book is intended for the average graduate student in our universities, rather than for the specialist in science or in history. The former class of readers has had in the past few treatises on the development of the plant sciences which were suited to his mental level. The latter class has had more treatises than they could read, regardless of the adjustment to their mental levels. A résumé of the subject is not a history unless it portrays to some extent the evolution of the plant sciences; how the beginning was made and how each grew out of some previous stage. It is important to know how we arrived at our present station on the road from Then to Now, as well as to know where we are now. Since science owes much of its development to man's natural curiosity about his environment as well as to his elemental need for food, clothing and shelter, I have started with the development of botany in a very early era and spent perhaps too much time in discussing the achievements of races at the dawn of history and subsequently. Those hairy and unkempt ancestors who devoted most of their lives to securing the material for the daily ration learned much about plants which has been handed on to us. Their biological skill has never been properly appraised. Men of the Stone Age

of culture met their requirements for food, clothing and shelter fairly well, but no one at any age of the world has fully gratified the instinct which we call "scientific". It is this instinct which characterized the development of the plant sciences and I have endeavored to show a few of the elemental stages in the history of the subject in the first part of this book.

The marvelous development of the biological sciences in the years when differentiation and specialization grew up constitutes the subject matter of the latter part of this book. I have tried to show the extraordinary development of the biological sciences in the years since the publication of "The Origin of Species" and the attempts at a better interpretation of natural phenomena which followed that epoch-making book. I have tried also to show the impact of the plant sciences on the affairs of the times, although fully conscious of my inability to deal competently with the matter. In this, as in other cases, contemporaneous history is the most difficult to write. It is easier to speak with assurance of first things than of last things. I have also attempted to bring to notice certain of the newer aspects of the twentieth century, in which the younger student must live and work.

After the men who assembled knowledge about plants, others came who ground lenses, through which they peered into the substance of the plants, and they were followed by others with more cunningly devised instruments which revealed not only cellular but molecular structure. Research work, which has become so intensively developed since the beginning of the twentieth century, is highly organized. The demands upon workers become more insistent with the passing of the years, eliminating thereby the tradition of the college professor in his ivory tower and his life which centered about the shady, cloistered walks of academic buildings.

At this point I wish to express my gratitude to a host of friends who have helped to alleviate the task of writing a book on such a broad field. My great indebtedness to Professor HERBERT M. EVANS for his never-failing inspiration through the writing of this manuscript, as well as for valuable typographic assistance which he generously furnished, will ever be gratefully remembered. Also I wish to express my thanks to other colleagues and friends whose friendly criticism of subjects with which they were far more competent to deal than I helped me to find my way through the wide range of subjects which I attempted to discuss. Among those who are to be mentioned in this connection are Dr. H. A. BARKER, Dr. LEE BONAR, Dr. A. S. CRAFTS, Dr. JEAN DUFRÉNOY, Dr. A. S. FOSTER, Mr. M. J. HAGERTY, Professor D. R. HOAGLAND, Dr. D. T. MACDOUGAL, and Professor RALPH E. SMITH. However, I must accept final responsibility for the manner of writing and for the statements herein contained.

It is also a pleasure to acknowledge the financial aid granted by the Council of the American Association for the Advancement of Science and the assistance furnished by the Works Projects Administration (official project 65-1-05-91B10). Acknowledgment will also be made in the proper places for the permission kindly given

by various authors and publishers to reproduce illustrations. I would thank Mr. C. C. TEBBUTT also for his faithful work on making the drawings from which many of the illustrations were made.

The work is documented but not encumbered with footnotes and side references. Believing that the graduate student should have things presented in such a way that he can see the end of the sentence from the beginning, I have not made many detailed references to sources. I have put into the reading lists subjoined to each chapter only such titles as I believed the graduate student can reasonably expect to read. The works cited frequently have long bibliographies, which the specialist or the student who wishes to pursue the subject may use if he wishes.

BERKELEY. *Autumn 1941.*

CONTENTS

Chapter 16.

Chapter 17.

Chapter 18.

Chapter 19.

Chapter 20.

Chapter I.

INTRODUCTION.

The study of the broader aspects of the plant sciences ought to orient the student and to counteract, to some extent the effects of the inevitable specialization which modern scientific curricula impose upon him. The flood of technical papers which continually surges over the tables and into the bays of the libraries dismays the student who wishes to evaluate the progress of science. To say nothing of the cultural, there is also practical value in having some background for judging things pertaining to a field of science, if one is to avoid grasshopper habits of thinking.

It may be important to consider the development of the plant sciences in four stages, which, although they are not chronologically distinct, are phases of the evolution of the subject.

A. Accumulation of information.
B. Verification.
C. Classification.
D. Interpretation.

It is unnecessary to elaborate these points. The first and possibly the second phases deal essentially with realistic concepts, while the others obviously introduce idealistic concepts growing out of the others. In a well-balanced piece of research all these stages are more or less apparent, and each is kept in its proper place.

A brief account of the development of the plant sciences aspires to give the reader an orientation of himself with respect to the diverse ramifications of the subject. If only moderately successful, it will show how the knowledge of plants has been obtained, bit by bit, from many sources. Since science is so largely an account of what has been learned about natural phenomena, there is value, for both the professional man and the layman, in some sort of an idea of how we have obtained this considerable body of knowledge which we possess. It may make us more patient when we survey the state of our present knowledge in which so many problems remain unsolved and others have not even been approached.

There is a danger that the results of modern scientific study may not only astound us, but blind us to the fact that discoveries equally stupendous have been made in other days. Those who would deny that there was any progress before the modern era certainly lack proper orientation and fail to realize that the results of modern science were dependent upon the antecedent results of uncounted workers. If we can see further than our predecessors it is because we are standing on their shoulders. It is perfectly evident to the informed observer that the complex results of the present supersede in many ways those of the past, but he should remember that, in all probability, they, in their turn, will be superseded by the results of the future.

The progress of botanical, as well as other, science has witnessed man's almost endless groping and fumbling. Seldom did he find the right path first, but only after he had made many detours and wandered up many blind alleys. He found that, as he ascended the hill of knowledge, the horizon expanded, and his ideas, which originally seemed so prominent, appeared ultimately as small mounds on the intellectual landscape.

One must get a long view if he can distinguish the real direction of man's progress in botany among all the devious, puerile ways in which he squandered his time and energy. And let it be remembered that we of this day may be, and probably are, beating about the bush or chasing rabbits as assiduously as our predecessors. The retrospective view of the development of plant sciences should engender a profound tolerance of others, because the ways of mankind are very uncertain at the best.

A brief acquaintance with the history of work in the plant sciences impresses one with the genius and character of those who, through many centuries, have studied the manifold aspects of the plant world. Believing that the student should associate a man with something more than his scheme for classifying things, I have sought to give vitality to outstanding men, no less than to recount their scientific accomplishments. We cannot know them only as pictures on a page, or as shadows moving along a wall, or as names perpetuated in genera and species. There were men with encyclopedic minds who wrote great books about the world and all its creatures, and there were sandalled friars who brought from some pilgrimage a few seeds in the folds of their robes. They led the way for the professor in academic garb bearing his precious degree, *magna cum laude.*

These men of whom I write in the first part of the book had to learn how to live in times of transition and of revolution, when thrones fell, or when pestilence stalked abroad in the land. They had to solve problems of human engineering in their day in addition to their botanical pursuits. They had to learn how to live with other people: kings, popes, caliphs, captains, presidents, deans (and perchance, wives). By and large they encountered most of the problems of authority and organization which confront the modern teacher or student. Their solutions of these problems interest us no less than how they investigated the mysteries of the organic world. I think that we shall see that most of the men who made the history of the plant sciences were strong, brown-cheeked, bright-eyed. A few suffered from bodily infirmities, it is true. Others poured out their lives too rashly on the altars of science. They contributed something to the advancement of plant science because they were willing to renounce transitory desires, or love of ease.

In spite of outward differences, all these men were suffused with a zeal for acquiring a better understanding of the organic world. Motives, as usual, were mixed, but they sought the truth. They were a wide-eyed and persistent race who saw where others were blind and found where others fumbled. Dominated by a reverence for life, nothing was so small or mean that it could be disregarded in the contemplation of an orderly concept of the universe in which they lived. Worship of life in a blind way is not science, but reverence for life is the beginning of wisdom.

A scientist is a product of the times in which he lives. Thus, one will see reflected in the lives of most of them ideas which were borne in by the tides of human affairs. At times original research flourished, at others it was subverted to so-called practical ends until it finally ceased to exist. When the implications of science began to be disturbing to the vested interests of church and state, scientists with their backs to the wall were often fighting for truth and freedom.

Specialization in science led to division of labor which, in turn, required the coöperation of others. Science is so essentially a social phenomenon that the individual accomplishes little without the help of others. It began to make noteworthy progress when one mind struck fire from another; when it used the help not only of other scientists, but also of printers, lens-makers, photographers, etc. From the time that BRUNFELS walked to Hornbach and back, to urge BOCK to publish his Herbal, there has been a spirit of mutual encouragement among the leaders in botany.

Scientific societies which afford a prompt means for communication of new results, also have developed an *esprit de corps* which has contributed greatly to the promotion of research.

Among the events of the 19th century which indicated the impetus given to biological studies by the publication of DARWIN's *Origin of Species* in 1859 none was more significant than the rise of international congresses. Students and professors had, since the Middle Ages, visited and studied in institutions outside their own countries, thereby demonstrating that true learning is not confined by national boundaries. It was perhaps natural that the enkindled interest in biological studies made men more anxious to broaden their fields of knowledge by conference with those who shared their interests in other countries. In so doing they were accomplishing more effectively the aims which they had had as individuals. International congresses were also a symbol of the new freedom that science found after the emergence of the great ideas presented by DARWIN.

The first international plant science congress was held in Brussels in 1864 and was designated as "Congrès International d'Horticulture". The small group of horticulturists and botanists held sessions which were probably rather informal. In 1865 another congress, attended by about 300 members, was held in Amsterdam, where 70 years later the last was held, with an attendance of approximately 1000 members. During that 70-year epoch two congresses were held in Brussels, three in Paris, and one in each of the following: London, St. Petersburg, Florence, Amsterdam, Genoa, Vienna, Ithaca, and Cambridge. Although hampered by international crises the spirit of coöperation in science steadily grew. Prominent scientists accepted positions of responsibility and unselfishly promoted the interests of the congresses.

The world came to expect important announcements of new discoveries, integration of ideas, the unification and simplification of terminologies, improvements in documentation, and similar objects. Perhaps the intangibles were the greatest products of the congresses, among which would come the inspiration received from conferences with colleagues, statements of research programs, and amity among scientists.

The development of a rational attitude toward science in the epoch mentioned was fostered, to say the least, by the congresses and symposia in which scientific workers participated with such enthusiasm. This attitude may be measured, however inadequately, by the increased funds dedicated to the purposes of science in all countries.

The growing spirit of international comity manifested by the creation of many sorts of associations may be seen also in the foundation in 1905 of the International Institute of Agriculture at Rome. Primarily concerned with questions of production and marketing, it was nevertheless of importance for the plant sciences, serving as a center of information on all subjects connected with agriculture and forestry. It was intended to keep pace with modern inventions of communications and transportation in marketing agricultural products and in the control of plant diseases.

The idea of the Institute originated with DAVID LUBIN, a Californian, who secured the necessary adherence of the principal countries of the world. The Institute was formally organized and furnished with a building by King VICTOR EMANUEL III of Italy. In 1910 there were 42 countries in the organization, each with its official delegate.

Among the publications having importance for the plant sciences, there were the monthly International Review of Agriculture (in five languages) and the International Review of the Science and Practice of Agriculture.

Since 1932 the Institute has been a consultant on agricultural matters for the League of Nations. It organized (1926) a World Forestry Conference, and (1929-30) a World Agricultural Census. To promote the study of Agricultural Ecology an International Institute was organized in coöperation with the Italian Royal National Academy in 1923, and formulated a comprehensive program of investigation based on fundamental scientific principles. The section on Plant Protection issues its monthly bulletin which, together with information on new and actual facts reported by different countries, contains a section on phytosanitary legislation and an up-to-date bibliography.

JACOB ERIKSSON, the Swedish phytopathologist, envisioned the necessity of effective international coöperation in plant protection and was active in creating the necessary implements for its operation. The International Institute of Agriculture in Rome invited the French Government to invite all contributing states of the Institute to an international phytopathological conference at Rome. In response to the call a conference was held in 1914 in Rome at which 39 delegates from 31 states (20 European and 11 non-European) were present. The aim of this convention was to organize an international convention acceptable to all states. The convention was intended to establish the principles for the organization of a phytopathological service in different countries. The act creating an international conference of phytopathology was written at Rome in 1914 and accepted by the delegates. Due to the decision of this conference, the question of international collaboration in order to combat the diseases of plants was in some degree - at least on paper - solved. By professional inspection and control, the principles were fixed for preventing as far as possible the spreading out of dangerous diseases from country to country.

Nevertheless, it was *a priori* easy to anticipate that it would be very difficult, if not impossible, to create an act which would obtain approbation from all countries of the world, especially since war intervened soon after the act was adopted. There was a tendency to isolate one nation from another and a disinclination for collaboration between different nations. As a result, only a minority of 9 states ratified the act.

It soon became apparent that plant pathologists did not possess enough information about some of the diseases to make the inspection work effective. The suggestion was made at several of the international congresses that there should be established a continental institute for plant pathological research somewhere in Europe, to facilitate investigations of these problems.

Whether the botanist attends seminars or the meetings of scientific societies, he must read the literature and by that means avail himself of contemporaneous, as well as historical results.

There were published in 1938 a total of 11,000 botanical papers, according to WELLENSIEK, or nearly 30 per day. Of this number 1/3 dealt with classification, nomenclature, and plant geography. Obviously a survey of that number of publications is impossible for any reader; however, he may avail himself of reviews in abstracting journals and of valuable indexes to current literature for information on any particular subject. Most of the 11,000 botanical papers which appeared in the year mentioned were written in such technical language that they could not be readily appraised by any, except a group of specialists, although the results presented in some papers may have had importance for the populace. For many years the intelligent reader has had difficulty in understanding what the workers in science were trying to say, and, as a result, the general public has been too long in ignorance of many matters which were important for general security and welfare. Some technical papers were often devoted extensively to matters of priority or nomenclature in which the reading public had small concern; other papers were written in a phraseology necessarily technical.

The cultural values of science for technical as well as nontechnical minds have begun to receive more adequate recognition. The willingness to accept guiding principles based on a body of accurate verifiable observations is preferred to opinions based upon traditional authority or outworn beliefs.

The beginning of the twentieth century saw a movement started to summarize and present scientific discoveries in a way which enriched the literature of science. Periodicals and books began to appear in all countries in which science was progressing. Their accounts of new discoveries gradually superseded the fantastic stories formerly written by hack-writers. The intelligent reader has asked that facts should be set forth as facts and not as fables. The improvement in accuracy of presentation came from the incursion of scientifically trained writers into the field, who have shown that truthful narratives may be fascinating reading.

Endowments to support a few of the interpretative periodicals were created by the year 1930 and societies sponsored other publications. Most of them however depended upon the sales of their output.

There has been and perhaps will always be a necessity for permanent records of technical work, published in a form readily understood by relatively few, and there has been developed a method of photographing manuscripts on reels of narrow film which obviates the slower and costlier methods of reproduction on the printing press.

It becomes increasingly obvious that the field of the plant sciences is broad and that some means of orientation is a paramount necessity. This fragmentary presentation of the history of the plant sciences is intended to guide students during the formative period to a better understanding of past and present trends, and to clarify the increasingly complex situation into which they will eventually be thrust.

Chapter II.

GARDENERS AND HERBALISTS OF ANTIQUITY.

The dawn period:- At what time and by what means plants of the earth and sea were discovered, tested, and utilized we have extremely fragmentary records. It is certain that it took a very long time, so long in fact that the wild progenitors of some plants are not now known. Settled abodes and communal life were impossible until man had begun to cultivate the land and to obtain a dependable harvest. Every important agricultural plant is a human achievement because it represents, not only discovery, but also profound modification of a wild species. The degree to which plants have been modified, whether consciously or unconsciously for human needs is a measure of man's ability to stabilize his environment.

The discoveries of plants and their uses began at some very remote period, probably in the Stone Age. Prehistoric men knew and utilized practically all the important foods of our time. They planted in localities where the harvest would be ample and where the distance from the tribal dwelling was not too great for purposes of protection and cultivation.

The starchy foods, then, as now, undoubtedly made up a large part of the diet. This class of foods comes from plants which grow rapidly, yielding food which is palatable, nutritious, and digestible. Wheat, rye, barley, rice, and oats were the cereals chiefly grown in the old world, and maize in the new world. The inhabitants of Switzerland as early as the Neolithic period, cultivated three kinds of barley and at least five kinds of wheat, four of which might be regarded as distinct species. One variety of wheat apparently had been brought from Egypt along with *Panicum* and *Setaria* which supplemented the other cereals.

The high value placed upon wheat by the more progressive races and the ease with which it could be carried on their migrations may account for the wide distribution of the plant. The existence of different names for wheat in the most ancient languages probably means that the tribes, before they had developed a language, migrated from their original home, carrying the precious seed. Whether wheat came originally from the plateaus of Central Asia or from the Nile valley, it has been for a long time in cultivation, and is preferred by the majority of the white race.

Legumes have also been cultivated for a long time by the people of all continents. Peas and beans are not only edible when green, but the dried seeds contain a maximum of nourishment in a small quantity. The vines and husks can also be used as fodder for domesticated animals.

The edible leaves and shoots of many other plants have long been utilized for foods. The esteem for bamboo shoots in China and the "Dish of Herbs" in other countries bears witness to the

importance of such foods among ancient peoples. Accustomed as we are to succulent and nutritious vegetables, it is not easy to realize that the stringy roots of wild parsnip or carrot should ever have been sought as food, yet from what we know of the food of savages we need feel no doubt on this point.

Men of those remote ages also knew, in addition to food plants, others which had remedial properties. Steeps and brews of leaves, or roots, or bark were administered for diseases of children and their parents. Poultices of the bruised leaves of particular plants, laid on a wound, staunched the bleeding and hastened the formation of a clot. Seeds of some plants had purgative properties, or power to allay pain, or to induce sleep. Not all their herbal lore was valid, - not every plant whose leaves had the shape of a hound's tongue would heal the bite of a dog, neither could every leaf shaped like a heart cure cardiac affections. But in a simple, trial-and-error way they began to learn the remedial properties of plants. Originally, every parent was undoubtedly something of an herbalist and ministered to his family, but as knowledge grew and tribal organization arose there were people who assumed superior knowledge of herbs and who kept supplies for use in time of need. These medicine men and the herbalists who collected medicinal plants were botanists of a sort, but different from the farmer or herdsman.

This chapter will give a brief survey of the history of the origins of some important phases of the plant sciences in a few races. It will show how conscious efforts on the part of men led to a knowledge of the plant world and ultimately to some important discoveries. The inception of a civilized life was largely dependent upon man's biological skill in domesticating and perpetuating both plants and animals.

Plant Lore of Assyria:- Assyria was in large part an alluvial plain deposited by the Tigris and Euphrates rivers. The waters of these rivers had been used from remote times for irrigating the soil of the fertile plain. All records indicate that agriculture developed early in Assyria and was successfully prosecuted for many centuries. Among the writers of antiquity who commented on the system of agriculture were HERODOTUS in the fifth century B.C. and PLINY in the first century A.D. who stated that wheat was cut twice and subsequently afforded good pasturage for sheep.

Remains of plants were not as well preserved in Mesopotamia as in Egypt, but some reliable information has been recently obtained about the cereals. From excavations of a prehistoric site near Nineveh carbonized grains of barley, and a primitive small type of emmer were taken in 1933. PERCIVAL says these are the earliest grains hitherto discovered in Mesopotamia and belong to a period 4000 B.C. or earlier.

When and where the Assyrians got their crop plants is not definitely known. Some were indigenous, others undoubtedly came from the Iranian plateau. TIGLATH-PILESER I (1130 B.C.) made it a matter of record that he had brought cedars and other trees as well as rare vines from countries that he had conquered and had planted them in the gardens of his own land. In addition to cereals, the Assyrians cultivated fruits, including apricots, figs, olives, pomegranates, quinces, and grapes.

The date palm, whose fruit was utilized in many ways, was one of the most important tree crops, it could be eaten fresh or dried, it yielded sugar, and the sap of the tree could be fermented to wine. The culture of the date palm in Assyria went back to an early time as shown by sculptures on very old temples. It was almost the only tree that grew there, and it grew in marvelous abundance. Stem, leaves, and fruit were all utilized. Its trunk was used for the columns and roofing beams of temples and houses, also for binding the brick walls of the cities; its fibers were twisted into ropes; its leaves woven into baskets; and its tender tips were boiled and eaten as a vegetable.

A scientific discovery of fundamental importance was made in Assyria, namely, sexuality in the date palm. Sculptures show that Assyrians artificially pollinated the spathes of the pistillate trees, and several Greek writers commented on this custom of the Assyrians. Knowledge of sexuality in plants remained at that point until CAMERARIUS made the discovery of sexuality in plants and GLEDITSCH showed that transfer of the pollen was necessary to fertilize the pistillate flowers of the Mediterranean fan palm. One must admit that the Assyrians and many of their successors wrongly applied the ideas of maleness and femaleness to other plants, such as *Cyperus* and mandrake, to which certain ideas of magical powers were also given.

An Assyrian herbal of the seventh century B.C. (THOMPSON 1924) gives a list of medicinal and semi-medicinal plants. Like many other herbals, it is a compendium of older ideas about plants intelligently and methodically arranged. A study of the document indicates that the doctors and chemists of Nineveh had a very respectable knowledge of plants and their uses. The author of the herbal made an attempt to classify the plants, beginning, logically enough, with the grasses and continuing with the rushes and *Euphorbias*. In other respects he was less consistent. For example, he grouped the *Papavers* and *Cucurbits* together because the names of the principal plants in those groups begin with the sign H U L, and he scattered composites throughout his entire series.

Two examples from the herbal will show how the subjects were treated:

GISIMMARU, Date Palm. Its "clean heart thou shalt chew in thy mouth." The inside of the very top of the palm-trunk is edible, having the color and consistency of celery heart. XENOPHON mentions it, saying that the soldiers ate the crown of the palm and were surprised at its appearance and peculiar flavor. . . .

The sap of a palm is obtained by cutting off the head of the palm and scooping out a hollow in the top of its stem, where the sap can gather. After six weeks the trunk becomes exhausted and is then cut down. Herein perhaps lies the explanation of the "palm from the north" (north, probably referring to some peculiarity of the rare palm not growing satisfactorily above Tuz Khurmati). Tuz Khurmati is the highest point at which the palm flourishes; above this the palm is practically worthless as a fruit tree. Down in the south, where the palm is cultivated for its fruit, this wasteful method would hardly be employed.

HAŠÂNU, Thyme, a drug for the lungs, to be chewed. A drug for the dyspnoea, to be drunk alone in oil and beer. Its smell revives an epileptic. Thyme is also used for hardness of breathing.

The names which the Assyrians gave their plants persisted for a long time and were carried, probably by merchants, into the western world. The following list will illustrate.

PLANT NAMES

Assyrian or Sumerian	*English*	*Western Language*
ARMÂNU	apricot	Armeniaca
AŠ	asafoetida	Asa
AZUPIRANU	saffron	(through Arabic)
AN. BAR	Liquidambar	(through Arabic)
HARUBU	carob	(through Arabic)
KUDIMERANU	cardamon	Kardamon (Greek)
KARŠU	cherry	Kerasus (Greek)
MURRU	myrrh	Murra
NUŠHU	almond	(Nux?)
PA. PA.	poppy	Papaver
ŠAMAŠŠAMMU	sesame	Sesamon

In course of time, all industries gave way to war and splendor, leaving only slaves to till the fields. All commerce passed into the hands of the alien Arameans of Syria. The rank and file of the armies also had to be filled with foreigners. In the seventh century B.C., the Empire was overthrown by the Medes. Inhuman cruelty, senseless brutality, and incredible mercilessness ended all Assyrian civilization.

Plant lore of Egypt:- The portion of Egypt traversed by the Nile is the seat of an exceedingly ancient civilization which, extending its branches, fostered the development of civilization in other countries. The unique behavior of the Nile, its periodic overflow and its deposits of fertile soil, need only be recalled to account for much of the rich development of human activities in this region. Six thousand years ago the Egyptians had a calendar year divided into three periods, Flood, Seedtime, and Harvest. "It is certain that Egypt had domesticated the wild ass, bred cattle, practiced irrigated farming, was using metals, had invented writing, and had developed government on a big scale, before northern Europe had seen the last of the Ice Age". (DORSEY 1931).

Food plants began to be cultivated in Egypt, or somewhere in the Fertile Crescent, at least seven, and possibly ten thousand years ago. Records of the botanical achievements of the Egyptians are, nevertheless, scanty where we should expect to find them abundant. The crops in Egypt were planted and cultivated presumably by the conquered natives, whereas epic poems were written and heroic events recorded by the transplanted kings of intruding dynasties. What we know has been obtained indirectly and not from any records such as the Chinese made. Fortunately, pictures on the walls of some of the tombs are in such good state of preservation that the plants can be recognized; and, better still, funeral wreaths and jars of food placed near the sarcophagi have remained unchanged for thousands of years in that dry climate. FLINDERS PETRIE found a number of funeral wreaths which contained more than twenty species in an almost complete state of preservation. Roses had been picked in the bud stage in order to prevent the petals from falling. The dried flowers were carefully soaked in water and could then be examined with ease. A few fragments of plants were accidentally preserved also in sun-baked bricks, in

addition to the straw of barley or wheat that was used to bind them.

HERODOTUS, the Greek historian, travelled in Egypt about 465 B.C. and left an entertaining account of what he learned.

"At present, it must be confessed, they obtain the fruits of the field with less trouble than any other people in the world, the rest of the Egyptians included, since they have no need to break up the ground with the plough, nor to use the hoe, nor to do any of the work which the rest of mankind find necessary if they are to get a crop; but the husband-man waits till the river has of its own accord spread itself over the fields and withdrawn again to its bed, and then sows his plot of ground, and after sowing turns his swine into it - the swine tread in the corn - after which he has only to await the harvest. The swine serve him also to thresh the grain, which is then carried to the garner". (RAWLINSON's translation).

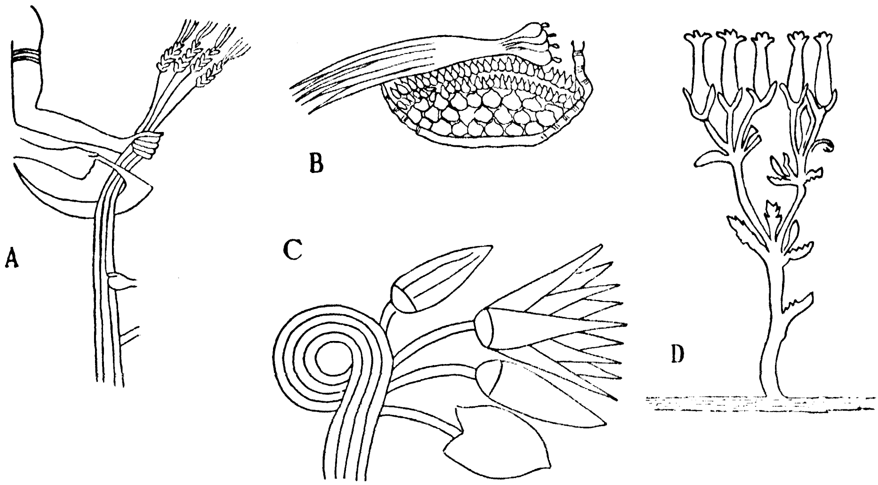


FIG. 1. — Egyptian tomb pictures. A. Reaping wheat (probably *T. dicoccum*) from ROSELLINI. The Rameum at Thebes. B. Basket of vegetables (probably onions and radishes) covered with a bunch of onions. Benihassan. C. Lotus flowers on offerings to the dead. XVIIIth dynasty. Deir el-Bahri. D. *Kalenchoë* sp. Temple of Karnak, Thebes about 1500 B.C.

Professor SCHWEINFURTH, a careful student of plants who resided many years in Cairo, recorded a wealth of interesting facts about the tomb-pictures and the plant remains in the tombs. In addition to the foods placed in the coffins, he identified many plants from the mummy-wrappings. He made a special point of the fact that the species found in the ancient tombs are identical with those growing in that locality today.

Although we know little of the people who domesticated or cultivated these plants, yet it is possible from the remains to form some idea of the fields, kitchen gardens, and orchards of Egypt before the time of ABRAHAM (2400-2200 B.C.). Pictures from the walls of the ancient tombs are important sources of information concerning plants. UNGER has reproduced many pictures of importance in which we see onions, figs, dates, and other foods. Dishes of food in the tombs included pottage made from lentils. *Asparagus* and artichokes, however, were incorrectly identified by some explorers and have not yet been indicated from ancient Egypt. The picture of so-called "artichokes" probably represent Romaine salad, according to KEIMER.

Examination of the contents of the oldest known human stomachs was made by ELLIOT SMITH, and by NETOLITZKY. The last meal eaten by these men 6000 years ago contained barley, millet, and tubers of the nut rush. According to Mrs. V. L. TÄCKHOLM this millet was not *Panicum miliaceum*, but *Echinochloa colonum* Link.

The assurance of a food supply has always depended upon the culture of cereals. The climate and soil of Egypt are well suited for the production of wheat, barley and millet. According to the ancient Hebrew chronicles, neighboring tribes went to Egypt in times of crop failure to buy grain. The Roman Empire depended largely upon Egypt for its supply of wheat. Although Egypt suffered crop failures at times, the water of the Nile made possible a fairly stable agriculture.

In the predynastic period the Egyptians cultivated wheat and barley, a period probably extending from about 5000 B.C. down to 3400 B.C. The wheat which was grown was a primitive form known as emmer (*Triticum dicoccum*) with flat ears having long awns. The naked grains are narrow and pointed at each end, distinctly different from the plump seeds of modern wheat. In an Egyptian tomb of the First Dynasty (3400 B.C.) an ear of bearded grain carved on ivory was found; this may have been barley, but presumably was emmer. Seeds of a naked wheat taken from an ancient granary have not yet been positively identified but is probably *Triticum durum,* according to PERCIVAL. Although UNGER found a small grained wheat in bricks supposed to date from about 3359 B.C. and identified it as *T. vulgare antiquorum,* SCHWEINFURTH found in the tombs no wheat other than the *T. vulgare* which is today cultivated in Egypt.

The cultivation of wheat as it is known today in Egypt antedates the invasion of the Shepherd Kings (?1700 B.C.), but the cultivation of the six-rowed barley (*Hordeum hexastichon* L.) is perhaps still more ancient. Furthermore the manufacture from barley of *booza,* a beer, appears to date back to the time of HERODOTUS (Fifth century B.C.). Wild barley and wild emmer grow at the present time in Palestine, Syria and regions near the Caucasus, according to PERCIVAL. These two cereals may have attracted the attention of the first cultivators and have been selected by them long before the dynasties of Egypt were formed. Emmer and barley have been found in prehistoric sites by BRUNTON at Badari and Montagadda, and by Miss CATON THOMPSON in the Fayoum desert, and in the intestines of prehistoric mummies by the Hearst Egyptian expedition. The cultivation of these cereals has been placed by some archaeologists as early as 10,000 or 15,000 B.C.

The procedure of the barley harvest is shown in figure 2. First, the standing grain was measured by a cord in order to assess the field for the dues of A m u n. Two men walked along the edges of the field, the foremost holding a reel adorned with the head of the god in ram form, his comrade held the other end of the cord. The owner followed in the rear. This simple computation, however, needed two scribes to book it, and a policeman with upraised club (center) to keep order. The second picture shows the method of harvesting the grain after the dues were settled. The ears were cut and carried off in panniers, leaving the stalks to be pulled up later (from DAVIES and DAVIES; Theban Tombs Series).

In addition to these cereals, the Egyptians brought into cultivation plants such as beans, lentils, radishes, melons, onions, and garlic. HERODOTUS mentioned several of them as articles furnished to laborers engaged in the construction of the Great Pyramid. There is no evidence that these plants were imported or used elsewhere at that time for food, and it seems fairly certain that they were homegrown.

The plants utilized in medicine by Egyptian physicians were numerous according to the Ebers and Hearst medical papyri. Of the two, the Ebers, coming from Thebes, bears the marks of riper scholarship and of a more systematic arrangement. It may have been one of a collection belonging to a great Theban priesthood.

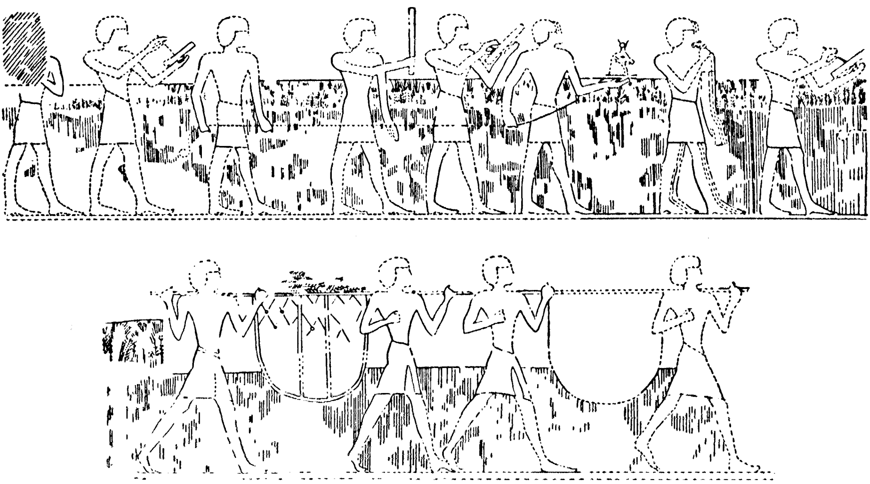


FIG. 2. — Harvesting barley in Egypt. Picture from the later tomb of Menkeheperrasonb. Fifth Mem. Egyptian Tombs series. 1933, Plates XVII and XVIII. See explanation in the text. By permission of the Egypt Exploration Society.

The Hearst papyrus, written in the period between the 12th and 18th dynasties was probably a reference book for local physicians. Among the plants mentioned by the latter papyrus are barley, beans, cedar, dates, grapes, lotus, myrrh, olives, sycamore, tamarisk, and wheat.

The use of fine linens and tapestries indicates that flax was cultivated from very early times, indeed, there are reasons to believe that it was obtained from Babylonia. A discovery of linen in MENES' tomb at Negada fixes the date in the First or Second Dynasty. A thread found in one of the bricks at Dahschur carries its cultivation back to nearly 4000 B.C. Seed capsules of flax are found in very early tombs, *e.g.*, by G. MÖLLER at Abusir el Melak (First or Second Dynasty), others have found them numerous in all periods. SCHWEINFURTH found seed capsules attached to their stalks in a tomb of the Twelfth Dynasty (2400-2200 B.C.). The Egyptian flax was apparently an annual form, since ancient pictures show that the plants were pulled instead of being cut.

The discovery and utilization of papyrus will ever be regarded as one of the greatest biological accomplishments of the Egyptians. The plant is represented many times in their pictures of river scenes. It was so characteristic that it was used as the symbol for

Lower Egypt, or North. Since the supply of wood was scanty, Egyptians constructed boats with bundles of the long flexible papyrus stems, and water-proofed them with bitumen. The "Ark of bulrushes" in which the infant Moses was abandoned was doubtless such a craft. Charcoal was made from the stems. The starchy rhizomes of the plant were cooked and used for food. The achievement of paramount importance in the history of civilization was the manufacture of paper from the pith of papyrus which facilitated the communication of ideas and the development of a culture which has been admired for thousands of years. HERODOTUS said:

The byblus (papyrus), which grows year after year in the marshes, they pull up, and, cutting the plant in two, reserve the upper portion for other purposes, but take the lower, which is about a cubit long, and either eat it or else sell it. Such as wish to enjoy the byblus in full perfection bake it in a close dish heated to a glow. Of the lotus, *Nymphaea lotus,* he said:

There is also another species of the lily in Egypt, which grows like the lotus in the river and resembles the rose. The fruit springs up side by side with the blossom, on a separate stalk, and has almost exactly the look of the comb made by wasps. It contains a number of seeds, about the size of an olive stone, which are good to eat: and these are eaten both green and dried. (RAWLINSON's translation).

The pomegranate, although probably introduced from Asia, was frequently represented in pictures in the old temples. There is no doubt but that it was highly esteemed by the Egyptians. MASPERO, in 1882, found the remains of pomegranate flowers in a tomb of the 20th to 26th Dynasties at Thebes. FLINDERS PETRIE found three unripe fruits in Hawara (Second to third century A.D.).

Records of the cultivation of the grape and of the making of wine in Egypt date back five or six thousand years. They appear for instance on the tomb of PTAH-HOTEP, who lived at Memphis about 4000 B.C. Paintings of vine cultivation and wine making are often met with during the Fifth Dynasty. Raisins are frequently found in the old tombs, also grape leaves and branches. RUBENSOHN found a mummy from the second century, A.D., whose head and neck were wrapped entirely in vine leaves and branches. Many interesting references to pomegranates and dates in relation to medical prescriptions are given in the Papyrus Ebers.

Many ideas in the Materia Medica of the Egyptians appear to have been borrowed later by the Greeks. A large number of the remedies mentioned by DIOSCORIDES may be found in the medical papyri and are prescribed for the identical diseases. Since the art of medicine in Egypt had reached a fairly advanced stage when the oldest medical papyrus was written about 1900 B.C., it necessarily implies a long development, probably from 3000 B.C.

In conclusion it may be said that Egyptian botany was empirical. Plants were domesticated, or were introduced from Chaldaea, their uses discovered, and grain was exported. Perhaps the fertility of the soil and the assurance of abundant harvests were unfavorable for extended intensive study by the intellectual men of the country. No herbals were written and few names of men who understood plants have come down to us. Civilization seemed to leap forward when agricultural complexes were adopted. The discovery of new and valuable food-plants and their cultivation was a stimulus which provoked the invention of collateral or subsidiary complexes.

"Once the technique of crops was discovered in the Nile Valley, for example Egyptian life began to blossom like a garden. Not that every "blossom" was beneficial to mankind; but life, freed of the haunting fear of want, began to blossom out in new fields of endeavor. Life was so rich and so easy that they could afford to spend an enormous amount of time on trying to make life eternal". (DORSEY 1931, p. 261).

The sabbatical year:- The Pentateuchal codes of the Hebrews required the people to allow the lands to lie fallow every seven years as well as to observe certain other rules concerning property. The Book of the Covenant does not specify that the same year should be observed by all districts and all individuals. In its essence it was undoubtedly the survival of a period through which almost every agricultural community has passed. Apart from the

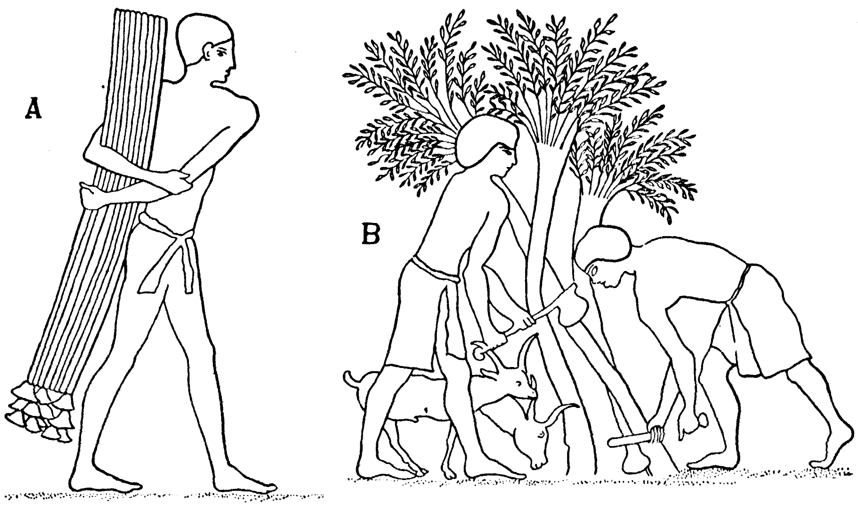


FIG. 3. — Egyptian tomb pictures. A. Man carrying a bundle of stalks of *Cyperus*, the Papyrus plant. Kum el Achmar. B. Destruction of date palm trees by enemies.

spiritual implications of the sabbatical year, the curtailment of grain production necessitated a septennial reduction in the number of live stock which, by culling out the unfit, resulted in improvement of the quality of the remaining animals. Furthermore, the decrease in the quantity of grain reduced the tendency of the people to trade with neighboring countries and served to prevent the accumulation of unwieldy fortunes. The year of fallow was also an unquestioned benefit to the land, by preventing exhaustion of fertility, weediness, and, in arid countries, conserved moisture.

Plant lore of China:- Everything which has been learned about the ancient Chinese indicates that they had a settled system of agriculture at a very early date and that they successfully domesticated and cultivated many Asiatic plants. In remote times the Chinese had already developed a system of fallowing the land. Instead of regular, permanent fields they had probably only temporary clearings which they abandoned at the end of a few years, leaving the natural vegetation to regain possession of the former fields while they cleared new areas.

The Chinese peasants' age-old custom of deserting their villages entirely from the middle of spring to the end of autumn and going to live in groups of three families each in communal huts erected in the midst of the fields may be regarded as a vestige of the time when the temporary fields were in the virgin forest, far distant from the village. The reclamation of the land from river and swamp was a long and painful process requiring the erection of dikes against inundations and the digging of canals to drain and dry out the soil.

All these tasks had been accomplished so long before the dawn of history that their very memory was lost, and they were believed to have been accomplished by heroes descended from Heaven at the beginning of the world — HUANG-TI, the Yellow Emperor; SHEN-NUNG, the Divine Plowman; and finally YÜ, the Great.

The fields, which were periodically re-allotted, formed blocks of approximately one square li (15 to 20 hectares), each forming one *ching* divided into nine equal lots cultivated in common by eight families. Each family kept for itself the cultivated produce of one lot while that of the ninth went to the king or to the feudal lord by way of tribute. Scattered and almost lost in the midst of the plain, little clusters of mud huts were erected in groups of twenty-five, - the winter dwellings of the peasants. These groups formed the smallest religious and administrative divisions.

No authentic writings on the customs of the agricultural communities of the earliest times in China are known, but subsidiary information may be obtained from some of the classics which show the agro-botanical basis of their civilization. In the subjoined translations of the Odes of Pin we get a picture of the life of Chinese agriculturists from as early as 1796 to 1325 B.C. (from LEGGE's translation).

THE ODES OF PIN

(*From The Chinese Classics. Legge Jas. vol. IV. Book XV Ode I*).

1. In the seventh month, the Fire Star passes the meridian:
In the 9th month clothes are given out.
In the days of (our) first month, the wind blows cold;
In the days of (our) second, the air is cold;—
Without the clothes and garments of hair,
How could we get to the end of the year?
In the days of (our) third month, they take their plows in hand;
In the days of (our) fourth, they take their way to the fields.
Along with my wife and children,
I carry food to them in those south-lying acres.
The surveyor of the fields comes, and is glad.

2. In the seventh month the Fire Star passes the meridian:
In the ninth month, clothes are given out.
With the spring days the warmth begins,
And the oriole utters its song.
The young women take their deep baskets,
And go along the small paths,
Looking for the tender (leaves of the) mulberry trees.
As the spring days lengthen out,
They gather in crowds the white southern-wood,
That young lady's heart is wounded with sadness,
For she will (soon) be going with one of our princes as his wife.

3. In the seventh month the Fire Star passes the meridian;
In the eighth month are the sedges and reeds.
In the silk-worm month they strip the mulberry branches of their leaves,
And take their axes and hatchets,
To lop off those that are distant and high;
Only stripping the young trees of their leaves.
In the seventh month, the shrike is heard;
In the eighth month, they begin their spinning;—
They make dark fabrics and yellow.
Our red manufacture is very brilliant,
It is for lower robes of our young princes.

4. In the fourth month, the small grass is in seed.
In the fifth, the cicada gives out its note.
In the eighth they reap.
In the tenth the leaves fall.
In the days of (our) first month, they go after badgers,
And take foxes and wild cats.
To make furs for our young princes.
In the days of (our) 2nd month, they have a general hunt,
And proceed to keep up the exercises of war.
The boars of one year are for themselves;
Those of three years are for our prince.

5. In the fifth month, the locust moves its legs,
In the sixth month, the spinner sounds its wings.
In the seventh month, in the fields;
In the eighth month, under the eaves;
In the ninth month, about the doors;
In the tenth month, the cricket
Enters under our beds.
Chinks are filled up, and rats are smoked out;
The windows that face (the north) are stopped up;
And the doors are plastered.
Ah, our wives and children,
Changing the year requires this;
Enter here and dwell.

6. In the sixth month they eat the sparrow-plums and grapes;
In the seventh, they cook the *k'wei* and pulse,
In the eighth they knock down the dates;
In the tenth, they reap the rice,
And make the spirits for the spring,
For the benefit of the bushy eyebrows.
In the seventh month, they eat the melons;
In the eighth, they cut down the bottle-gourds;
In the ninth, they gather the hemp-seed;
They gather the sowthistle and make firewood of the Fetid tree;
To feed our husbandmen.

7. In the ninth month, they prepare the vegetable gardens for their stacks,
And in the tenth they convey the sheaves to them;
The millets, both the early sown and the late.
With other grain, the hemp, the pulse, and the wheat.
Oh my husbandmen.
Our harvest is all collected.
Let us go to the town, and be at work on our house.
In the day time collect the grass.
And at night twist it into ropes;
Then get up quickly on our roofs;—
We shall have to recommence our sowing.

8. In the days of (our) second month, they hew out the ice with harmonious blows;
And in those of (our) third month, they convey it to the ice houses,
(Which they open) in those of the fourth, early in the morning,
Having offered in sacrifice, a lamb with scallions.
In the ninth month, it is cold, with frost:
In the tenth month, they sweep clean their stack-sites.
The two bottles of spirits are enjoyed
And they say, (Let us kill our lambs and sheep,
And go to the hall of our prince,
There raise the cup of rhinoceros horn,
And wish him long life,—that he may live forever.)

There is a tradition that the Emperor SHEN-NUNG, who reigned about 2700 B.C., is the Father of Agriculture and Medicine. He is supposed to have invented the plow and the plowshare, to have sowed first the five kinds of grain, and to have composed the first treatise on medicinal plants in a work known as Shên Nung pên ts'ao ching, the classical herbal of SHEN-NUNG. The first mention of this work occurs in the bibliographical section of the Chien Han Shu (History of the Former Han dynasty, B.C. 206 - A.D. 24) in which it was said that the herbal of SHEN-NUNG consisted of 20 chapters. It is not known exactly at what time the Shên Nung pên ts'ao ching was first written down, but there can be no doubt that it is one of the most ancient documents of Chinese materia medica. In the centuries which followed, copyists and transcribers sometimes added references to additional plants.

SWINGLE found a valuable Japanese reprint of this ancient Chinese work published about 1625, written by MIU HAI-YUNG, a native of Ch'ang-shu in the Soochow prefecture, entitled Shên Nung pên ts'ao ching su.

We may assume with a high degree of certainty that all plants mentioned in the medical herbal of SHEN-NUNG and in other early works are indigenous to China and have not been introduced from other countries. It was not until about 120 B.C. that the Chinese became acquainted with the distant parts of Asia, especially western Asia. Probably all plants designated in Chinese writing by one peculiar character are indigenous.

Mr. HAGERTY, translator of Chinese in the United States Department of Agriculture, has made translations from the works under discussion. The following excerpts from writers are of singular interest, not only because they concern a well-known fruit, but because they show that some supposedly modern methods of insect control have had a vogue for many centuries in China, *e.g.* Chi Han (Description of the flora of the southern regions, 290-307 A.D.) stated:

The Kan orange (*Citrus nobilis* Lour.) belongs to the chü (*C. sinensis* Osbeck) class. It has a sweet delicious flavor which is especially remarkable. There are yellow and deep red fruits. The deep red are called hu-kan, or pot mandarin oranges. . . . The people of Chiao-chih (Cochin-China) use mat bags in which they store ants and sell them in the market. The nests of these ants are like thin silken floss. The mat bags are attached to the branches and leaves and when the ants are inside, they are removed and sold in the market. These ants are of reddish-yellow color and larger than ordinary ants. In the southern regions, if the mandarin trees are without these ants, their fruits will be injured by swarms of boring insects and there will not be one perfect. . . . At present there are two mandarin trees in the Imperial Garden called

Hua Lin Yuan and when these bear fruit the emperor commands his ministers to hold a banquet beside the trees where he gathers and dispenses gifts of the fruit. (Transl. by HAGERTY).

There can be no doubt that most of the oranges are indigenous to China and have been cultivated from remote times. Each species or variety bears not only a different name, but is mentioned in several ancient works. Mandarin oranges and pummeloes were mentioned in the tribute of Yu from the province of Yang-Chow (2300 B.C.). The lemon tree is frequently raised in a dwarf form in pots as an ornamental shrub and also for its fruits at Peking. It is called Siang-t'ao and may have been introduced, since this name does not occur in ancient books.

The orange and certain other fruits in China were sometimes called "wild", or "mountain" fruits, not because they were undomesticated, but because of the method of cultivation on mounds. HAGERTY suspects that this usage of the word was based on an ancient belief that it was best to plant fruits which had seeds or stones on mounds or hillocks. He refers to passages in LI SHIH-CHEN's Pên ts'ao kang mu which confirm this idea.

Tea (*Thea sinensis*), the most renowned among Chinese cultivated plants, is now well known by the peoples of a large part of the world. Its culture has been said to date from the sixth century A.D., but there is good linguistic evidence to indicate that tea was used both medicinally and as a beverage at a much earlier period. As even today the Chinese use the leaves of plants or trees other than *Camellia* species to make the infusion called "ch'a", it is likely that they did likewise in ancient times, therefore the question is somewhat complicated. LINDLEY stated that the only country in which tea has been found in a wild state is Upper Assam, and added that a Japanese tradition favors the supposition of its Indian origin. The Chinese appear to know nothing of this legend, however, and the Pên-ts'ao states expressly that in China wild growing tea can be found.

With the aid of philology it is possible to trace a number of origins of Chinese plants. The pomegranate and the common pea came from western Asia. The carrot, a favorite vegetable of the Chinese, was first brought from western Asia to China at the time of the Yüan Dynasty (1280-1368) according to the Pên-ts'ao hence the name, Western Rape.

The work of plant selection and cultivation often received the attention of the rulers, according to ancient records. The Emperor KHANG-HI (1662-1723) related how he once noticed in a peasant's field a rice plant which had produced mature seed much earlier than the rest of the crop. He ordered his servants to gather the seeds of the precocious plant and he propagated it in his own garden. He concluded his account of the selection as follows:

> The grain is long and of a rather reddish color, but of a sweet perfume, and a very pleasant flavor. It has been named *yu-mi*, or "Imperial rice", because it was in my gardens that it was first cultivated. It is the only kind that can ripen north of the Great Wall, where the cold begins very early, and ends very late, but in the provinces of the south, where the climate is milder, and the soil more fertile, it is easy to obtain two harvests a year from it, and it is a sweet consolation to me to have procured this advantage for my people.

The Chinese gained knowledge empirically which proved to have enormous importance for others as well as for themselves. A small desert plant called "Ma Huang" has been known in China for thousands of years. It was collected and used for the alleviation of asthma, hay fever, and other affections of the nasal passages. The plant is *Ephedra* and is valuable for its content of the alkaloid ephedrine. Two species of it are found in China, namely, *E. sinica* Stapf; and *E. equisetina* Bung., which yield the commercially important alkaloid now known and widely used as the hydrochloride.

Chinese plant lore developed under conditions such that the knowledge obtained has never been widely dispersed, but has been to a large extent a racial culture. One who studies the subject will undoubtedly be impressed, however, by the success of the people in learning the flora of their region. Certainly, their work compares favorably with that of DIOSCORIDES who had much the same object in mind.

After a long period in which the most elementary things were learned about plants, the Chinese incorporated their plant lore into their social and economic life, as shown by the importance of the belief in the Emperor SHEN-NUNG. Impelled to continuous activity by population pressure and by recurrent famines, they have searched, tasted, collected, and identified the rich flora of eastern Asia. Their botanical productions were the marvel of occidental travellers who eventually found and carried them to many other countries. Since Chinese botanical literature is not widely known, even in China, the formal records of the accomplishments of these early students of plant lore have not reached many great libraries, since for many centuries the manuscripts could be reproduced only slowly and expensively.

Plant lore of the American Indians:- Fortunately for the study of cultural history, the races which inhabited the Americas when discovered by Europeans were in the Stone Age. We are able, therefore, to obtain some ideas from them about the technics of discovery and domestication of certain plants and to judge the amount of time required for the achievements.

The Nahuatl tribes of Mexico had developed a great scientific interest in plants as well as a knowledge of their economic properties. At the time of the conquest (1520) none of the nations of Europe were much superior to the Mexicans in botanical lore, for they had established a botanical garden on a more elaborate scale than had then been attempted in Europe.

In one of his letters to CHARLES V, HERNANDO CORTES commented on the trade in dried roots and medicinal plants in Mexico. "There are houses as it were of apothecaries where they sell medicines made from these herbs both for drinking and for use as ointments and salves". Not only had they acquired scientific and economic interest in plants but they had developed an aesthetic appreciation of plants for their beauty alone. Flowers were then cultivated extensively in the Valley of Mexico and sold in great quantities in the markets for the adornment of houses and temples. This love of flowers has persisted to the present time, and flowers still occupy much space in the markets. No one can fail to be

impressed with the great number of words in the Nahuatl language which have the termination "Xochitl", meaning "flower".

The existence of a systematized body of botanical and pharmaceutical knowledge is attested by the Badianus Manuscript written in 1552 by two Indians and given an interpretative translation by Dr. EMILY W. EMMART (see reading list at the end of this chapter). The richly illustrated manuscript was written in Aztec by one of the Indians and translated into Latin by the other. This herbal contains the earliest information about the plants used by those people for narcotics, emollients, astringents, purgatives, tonics, etc., and, moreover, gives directions for preparing and using them, since both wild, and garden plants are listed for these purposes, it is evident that there was an extensive trade in herbs.

Maize:- We may not assume that man has been present on the American continent an indefinite time; he arrived perhaps not more than 10,000 years ago. Since there is evidence that during at

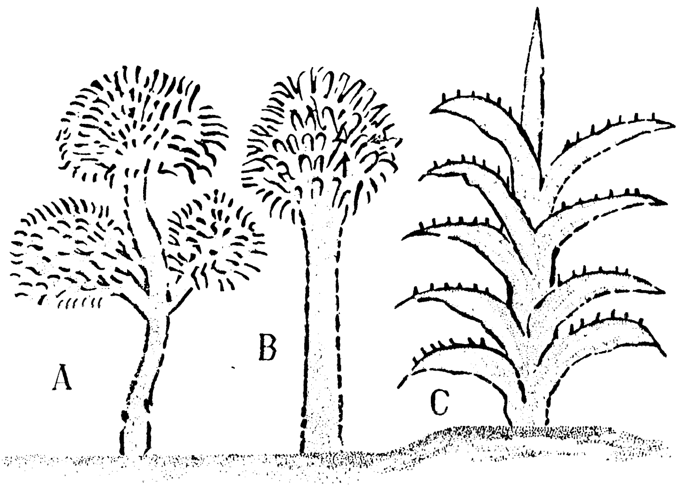


FIG. 4. — Plants from a Mexican picture-chronicle of 1530; yuccas (yçotl) and agave (metl). (Facsimile by QUARITCH 1890).

least half this period maize (*Zea Mays*) existed in its present high state of specialization, man must be credited with the ability to have produced this plant from very unpromising material and to have disseminated it over two continents in about 5,000 years. There can be little doubt that, in the Americas maize was the most important source of starchy food for a large part of the aboriginal population since it grows quickly and produces a large amount of food per acre. Europeans became acquainted with maize after the expedition of COLUMBUS to Cuba in 1492, who found it cultivated there by the Indians. The word maize which COLUMBUS adopted for this cereal is derived from *mahiz,* the name used by the Haytians.

The most ancient maize is that of the pre-Incas of Peru. Ears well preserved in the tombs of these people appear to belong to the varieties which are grown in those regions today, thus demonstrating that in the course of many generations there has been no appreciable change. Nothing suggesting a feral maize has ever been found, and it can only be concluded that this cereal attained

its present form earlier than the pre-Inca burials. Maize has also been found in old burial sites in Utah and in the mounds of the Ohio valley, resembling that produced by the Indians of those regions in modern times.

A remarkable instance of the antiquity of maize was given by DARWIN who, at Tacna-Arica, Chile, found ears of maize and 18 species of marine shells buried in soil, now at least 85 feet above the level of the sea. Pre-Inca burial vases on which maize was used as an object of decoration have been found in very ancient graves at Chimbote, Peru, and, incidentally, inform us concerning the varieties of maize known to the Indians of that time.

In Mexico the esteem for maize is indicated by the maize cult of the goddess CINTEUTL whose name was derived from centli the name given maize by the Toltecs. The first fruits of the maize harvest were offered to CINTEUTL as were the first fruits of the grains to her Greek counter-part, CERES. The gods of maize in Mexico enjoyed a prestige no whit less than those of rain or war but were regarded with affection rather than fear. The Aztec tribute lists show that maize was one of the important items collected annually from the subject communities.

The problem of the ancestry of maize has not been solved definitely. The plant has never been found growing in a wild state, indeed, it seems poorly adapted for that mode of life since it is unable to perpetuate itself except in cultivation. The nearest living relative of maize is the grass *Euchlaena mexicana* which the Mexicans commonly call teosinte. It grows in Mexico and Guatemala with a curiously discontinuous distribution and with an altitudinal range of from three to five thousand feet. In Mexico it grows as a weed in the margins of maize fields, but in Guatemala it is found in a wild state, wholly independent of cultivation. Both maize and teosinte have a chromosome number $2n = 20$, and hybridize readily. Botanists have assumed that maize originated as a mutant of teosinte, and that the mutant had some value as human food. Unfortunately, no proof of this theory has been obtained, other theories likewise lack confirmation.

The region in which maize originated is not now definitely known. The question is complicated by the fact that maize has never been found in the wild state and that its immediate progenitor is unknown. The opinion of botanists who have studied the question is not unanimous. If we assume that maize developed from teosinte (*Euchlaena mexicana*) both of which have 20 diploid chromosomes, it seems logical to regard Mexican and Guatemalan uplands as the home of maize especially since teosinte is indigenous there. KEMPTON found that the center of teosinte is at present around San Antonio Huxta in northwestern Guatemala where it occurs as a wild plant wholly independent of cultivation.

Upon the basis of extensive morphological and cytological researches MANGELSDORFF and REEVES have formulated (1939) a theory of origin of maize which started with an ancestral form belonging to the *Andropogoneae.* They consider that the modern type of maize is a domesticated variation of a wild *Zea mays* which descended with *Tripsacum,* but by a different path, from that common remote ancestor. They are inclined to regard *Euchlaena* as a plant of recent origin which had no part in the genesis of maize.

If we assume that a cultivated plant originated in the region where it later shows the greatest diversity, it seems logical to regard Peru as the home of maize. VAVILOV and his associates found in that country the greatest multiplicity of types. If maize had been carried from the point of origin into a mountainous country having a variety of soil and climatic conditions, that country would in time contain a multiplicity of types and hence a great variety of species. This is precisely what one finds in the steep and narrow valleys of Peru. On the other hand, no plants have

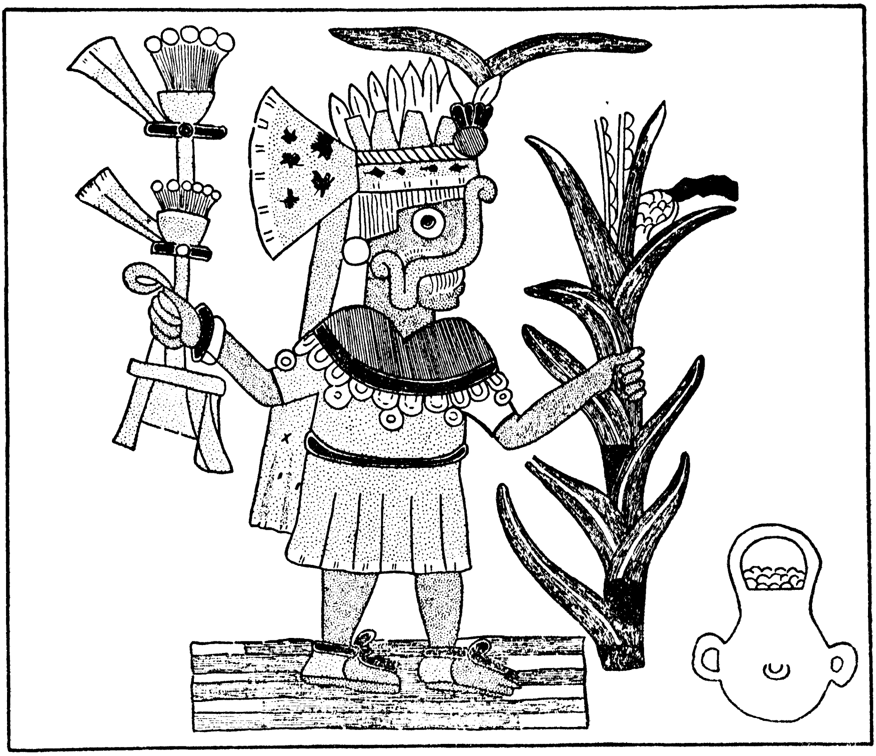


FIG. 5. — TLALOC, Aztec god of rain, with stalk of maize in one hand and a jar of maize at lower right. From NUTTALL, ZELIA, The Book of life of the ancient Mexicans.

been found in Peru which might be considered as the real or potential ancestors of maize, consequently the evidence that maize originated there is rather weak.

Historically speaking, we may regard with some confidence the incontrovertible evidence that this valuable plant was brought into cultivation and perpetuated by tribes which were in the Stone Age of civilization and that it has been a staple article of food since that time.

Whatever its origin, the plant went through a long process of skillful cultivation and selection performed entirely by the American Indian. We cannot fail to be impressed with this achievement of a race of men who had not emerged from the Stone Age when the work was done. In the course of centuries, the Indians had produced varieties adapted to various soil and climatic conditions as well as for special purposes. They grew Flint corn which ma-

tured in a short growing season in the North Atlantic seaboard, and another kind in the south. They had Dent corn and the small-eared, large-seeded Cuzco corn. The white race has produced no noteworthy varieties of maize in the four hundred years they have cultivated the plant, having merely adopted the maize they found growing in the fields of the Indians. The degree of differentiation was so great that each group of Indians, indeed often each family group, had its own varieties, differing in many respects from those of neighboring tribes, the differences becoming greater in proportion to the distances separating the tribes. Maize of a particular color was required for many ceremonial purposes and the tribes planted the fields at some distance from each other, so that there would be no cross pollination. An Aztec codex has been found showing the stages in the development of the maize plant from planting to harvest. From the character of the headdress of one figure in the codex, it seems evident the production of pollen as a feature in the production of maize was recognized. The termination of the headdress of this figure suggests pollen grains adhering to a highly conventionalized tassel.

Thin cakes of maize bread, called tortillas by the Mexicans, *tlaxcalli* by the Aztecs, accompanied by beans and peppers, and washed down with drinks made from maguey or cacao were the standard diet of the Aztecs and other tribes of America. They called the dried ears of maize *centli,* and the shelled corn, *tlaolli,* maize in the milk, or roasting ear stage, was called *elotl.* Mush or gruel called *atolli* was made from the seeds. To make it the seeds were hulled in a lye made from wood ashes, washed, mashed, and boiled in water. It was variously seasoned or sweetened, and eaten either hot or cold.

Spanish writers have given accounts of how the Indians "planted four or five seeds in hills which were spaced at the distance of a pace from each other", and the Indians of the Atlantic coast followed almost the same planting practices. The planting and cultivation of maize in the fields were carried out by hand labor with the assistance of primitive tools. The details of the cultural operations varied with location and with tribal mores.

Early writers on aboriginal agriculture frequently commented on the care bestowed on the fields of maize and beans. WOOD (1629) in "New England Prospect" wrote that the Indians kept the field "so cleare with their Clamme shell-hooes as if it were a garden rather than a corne-field, not suffering a choaking weede to advance his audacious head above their infant corne, or an undermining worme to spoile his spurnes".

A large part of the labor of cultivation was performed by the women, who apparently were adepts in the art of maize culture, especially in the manner of extirpating weeds without injury to the maize roots. CARRIER (1923) emphasized some of the important principles of tillage observed by the American Indians. The art of tillage was undoubtedly better practiced by them than by any other race with the exception of the Chinese. It will be recalled that the principal cereals of Europe at that time, were broadcasted and received no tillage.

Squashes were also grown and constituted an important part of the food supply of the North American Indians. These plants were usually grown in their cornfields just as yellow pumpkins are

now grown. The graves of Peru and the cliff dwellings of Arizona contain gourd seeds and implements made of gourds.

Potato:- The discovery and domestication of the potato (*Solanum tuberosum*) is another botanical achievement for which the American Indians deserve great credit. Lacking written records of their ancient cultural activity, we must rely on such materials as have been found in the burial sites in Peru and Chile. Desiccated tubers and potato-vases are sometimes found in association with the mummified bodies of prehistoric men. Although the evidence is scanty, it is important to note that in no other part of the world can one find evidence of ancient potato culture. The dispersal of the plant from South America has occurred only since the sixteenth century incursion of Europeans into South America.

On the high barren plateaus and lofty valleys of the Andes, to which the tribes of some legendary age migrated, life conditions were severe. In place of the diversified flora and fauna of the tropical forests there were treeless, wind-swept slopes on which the principal plant growth was a coarse *Stipa* grass. Community life in settled abodes was possible there as a result of an agricultural technic in which the potato played an important part. Today, as then, the Indians in this locality live in thatched stone huts near their fields or their rock-walled terraces. All work in the potato fields was done by hand and all hands worked.

Although various species of wild tuber-bearing *Solanums* grow as far north as Colorado, nowhere were they utilized as crop plants, although at times the natives ate them. We do not know why the tribes which penetrated into the western part of South America seized upon *Solanum* and developed a ruderal plant, while the same or related folk north of the equator developed maize instead of the potato. More than ninety varieties of the Andean potato differing from one another in color, size, shape, flavor, and earliness are cultivated by the natives today. Since the potato was not widely dispersed until after the Europeans came to America, it may be assumed that the actual discovery and utilization had occurred only two or three thousand years previously. The Indians also devised a method of drying the potatoes which was certainly an economical way to store the crops, since the dried potatoes could be kept for long and were also easier to transport over the steep mountain trails.

Evidence of skill in plant breeding or selection is afforded by the characters of potatoes capable of growing on the bleak cold plateaus of Peru and Bolivia, where it forms the chief food of the people. To meet this condition the Indians cultivate varieties which withstand lower temperatures than the ordinary potato and the short day environment. VAVILOV identified and named these varieties, *S. Ajanhuiri* and *S. Juzepczukii* which resemble the ordinary potato except that the first has a chromosome number $2n = 24$ and the second, $2n = 36$. If the latter is a hybrid of two distinct species, one of which is capable of withstanding low temperatures, we may conclude that the Indians possessed not only a high degree of intelligence, but also a ponderable agricultural background. As a measure of human skill it commands more attention than it has received.

The history of the cultivated potato in ancient times was not recorded for many reasons, but the people have preserved some

of their ideas in pottery. Jars and vases which convey many important points about the ancient potato have been found in the graves and old village sites. Potatoes are first mentioned in European literature in a letter from PETER MARTYR to Pope LEO X descriptive of the products of Darien.

> There are certain roots which the natives call potatoes and which grow spontaneously. The first time I saw them, I took them for Milanese turnips or huge mushrooms. No matter how they are cooked, whether roasted or boiled, they are equal to any delicacy and indeed to any food. Their skin is tougher than mushrooms or turnips, and is earth colored, while the inside is quite white. The natives sow and cultivate them in gardens as they do the yucca . . . and they also eat them raw. When raw they taste like green chestnuts, but are a little sweeter.

The first published account of this plant in America was written by PEDRO DE CIEZA DE LEÓN who in 1538 found the potato in the upper Cauca Valley in what is now Colombia, and afterwards at Quito. He succintly stated that many of the villages which he saw were in territory so high and cold that maize could not be grown and that the principal food crops were *papas* (*Solanum tuberosum*) and *quenoa* (Seeds of *Chenopodium quenoa*). The name of CIEZA DE LEÓN's work was Chronica del Perú, a journal which he wrote from night to night while his comrades were sleeping. In this he describes *papas* as "a kind of ground nut which when boiled becomes as soft as a cooked chestnut but which has no thicker skin than a truffle". Afterwards in writing of the elevated Callao region the plant is mentioned in greater detail.

> The inhabitants in that part of the world live in villages surrounded by cultivated fields, the principal crop of which is papas, which I have already stated in this history are like turmas de tierra. These they dry in the sun and keep from one harvest to another. And they call this *papa* after it is dried, *chuno*, and among them it is esteemed and held precious for they have no ditches like many others in this kingdom to irrigate their fields and if there is a dearth of natural water to make their crops, they suffer from a lack of food and work, unless they are provided with this sustenance of dried papas. And many Spaniards have become rich and returned to Spain prosperous only from carrying *chuno* to sell to the mines of Potosí.

ACOSTA, writing forty years later, also commented on the fact that the climate of the elevated portions of Peru was so cold and dry that cereals could not be grown, yet potatoes were generally cultivated.

The original habitat of the potato is a matter of paramount importance for many reasons, but is not definitely known. All evidence so far obtained agrees in locating the original home in South America. On the basis of personal exploration, WIGHT concluded that the plant from which our potatoes have descended was a native of the central Andean region, but he is convinced that *Solanum tuberosum* now grows only under cultivation. He says:

> Every reported occurrence of wild *Solanum tuberosum* that I have been able to trace to a specimen either living or preserved in the herbarium has proved to be a different species. In fact, so far as the herbarium material is concerned, I have not found in any of the principal herbaria specimens of *Solanum tuberosum* collected in an undoubtedly wild state. After a century and a half of intermittent collecting, there is no botanical evidence that the species is now growing in its original indigenous condition anywhere.

WIGHT is firmly convinced that *S. tuberosum* does not now exist in a wild state in Chile, but that does not preclude the possibility that it was at some remote time indigenous. No archaeological data which establish the date that potatoes were brought into cultivation have yet been reported from Chile. We find, however, that although the Chileans had a native name for the wild bitter-tubered variety, "Maglia", they borrowed the Peruvian name, *papas,* for the potatoes they cultivated. Since the food problem in Chile was less acute than in Peru and Bolivia, less emphasis was apparently placed on its culture and the Chilenos suavely adopted the Peruvian name.

A variety of *S. tuberosum* which has a chromosome number $2n = 24$ and yellow flesh occurs in cultivation in the Andes. This is called "papa amarilla" and on account of its flavor is a great favorite with the natives. Evidence from pottery found in burial sites indicates that this variety, or one bearing similar tubers, was cultivated as long ago as 800 A.D. The cultivation and per-

FIG. 6. — *Xanthosoma* (*Huacalxochitl*), an illustration from the BADIANUS Manuscript, 1552. The plant was cultivated in Mexico and highly prized by the Aztecs for the relief of angina and for other maladies. Reproduced by permission of the Johns Hopkins Press.

petuation of this variety is further evidence of a planned selection since the ordinary variety of the Andes has a chromosome number of $2n = 48$.

VAVILOV and his associates concluded from various lines of evidence that there were two centers of distribution of the potato in South America; one on the plateaus of Bolivia and northern Peru, another on the island of Chiloe and the adjacent mainland of Chile. In the first mentioned localities the soil is poor, rainfall is scanty and the days are short; in the second, the soil is rich, rainfall is abundant and, during the growing season, the days are long. They regard the potatoes of these two localities as distinct species, each having 48 diploid chromosomes. They designate the Bolivia-Peruvian species as *Solanum andigenum,* and the Chilean as *S. tuberosum* and consider that the latter is identical with the potato cultivated in North America and Europe. The fact that the potato thrives in the cool, moist climate of northern Europe lends support to this assumption. There is no historical proof,

however, that the potato which was carried to Europe towards the end of the sixteenth century came from Chile and not from Peru.

The foregoing sketch of the discovery and selection of the potato should be supplemented by an account of the cultural methods by which the Indians obtained sufficient production of tubers to keep themselves alive. The Inca nation not only developed agriculture, but also built imposing buildings and cities, developed a social and political structure, and lived at peace with their neighbors. Their skill in the arts of civilization is the marvel of all who have studied it.

WIGHT (1916) has stated that the Indians of the mountain regions of Peru and Bolivia today, as in ancient times, work the soil with wooden hand tools. Several men working together dig the soil with spades which are more like bars than spades. Women turn over the clods thus pried up and build a sort of ridged bed on which the potatoes are planted. In the island of Chiloe where rainfall is more abundant and the soil more fertile, the cultural operations are simpler. The native, using a sharp stake, makes holes in the ground from 16 to 18 inches apart. After inserting a tuber in each hole he presses back the soil with his foot, pries up clods, and throws them upon the row. After crushing these clods with mallets, he considers the planting operation to be complete. He may hoe the soil once or twice during the season, but no further work is performed until he digs and carries away the crop.

With these primitive methods, the South American Indians were able to set up a permanent agriculture and for centuries to perpetuate without deterioration a plant which has been valuable in many parts of the world.

When and how potatoes were carried from South America to Europe is not definitely known. Most of the accounts formerly given have been discredited by later historians. It seems safe to assume that Spanish travellers carried them thither from Peru along with other loot. There is no evidence however, that CAVENDISH or DRAKE introduced potatoes into Europe. The former navigator reached Plymouth on September 9, 1588, but CLUSIUS had received potatoes on January 26, 1588, and planted them in the Botanical Gardens of RUDOLPH II in Vienna. In his Historia Plantarum, published in 1601, he stated that potato culture was established in many gardens in Italy earlier than 1588. We may infer from various bits of evidence that the potato had been brought to Spain as early as 1570.

One of our choice fruits, the avocado, was esteemed by the Indians for its food and medicinal properties. The Aztecs called the tree Ahuacaquahuitl, which the Spaniards shortened to Ahuacate, from which the Americans have departed by calling it avocado. In addition to its use as food it was supposed to possess therapeutic properties. A decoction of seeds, or a piece of a seed placed in the cavity of a tooth was supposed to cure toothache. A decoction of leaves or bark of the tree was reputed to have as many beneficient uses as a person had ailments.

The limitations of space forbid the discussion of further records of the discovery, selection, and perpetuation of plants by the people of antiquity. This brief survey may give the reader a useful conception of the initiation of man's acquaintance with the vege-

table world. The acquaintance was many times begotten of necessity, at other times it originated in superstition, and often came after failures due to various conditions over which man had no control. Out of it, however, came a knowledge of plants. Although it was almost entirely empirical knowledge, man had accumulated a store of information which enabled him to obtain the daily ration for himself and his family and, in many cases, to acquire the amenities of civilized life. Our progenitors developed a biological skill which is no less meritorious than our mechanical skill. From them we of the present day obtained the plants from which food and textiles are derived. Our age-old freedom from the necessity of winning our foods from the wilderness may have dulled our appreciation of the achievements of the herbalists and gardeners of the past. Today the emphasis is laid upon machine technics, but for centuries man had developed biological technics which underlie our whole complex modern life.

REFERENCES:-

BADIANUS Manuscript: An Aztec herbal of 1552. Translated and annotated by EMILY WALCOTT EMMART, 1940. Johns Hopkins Press, Baltimore.

BRETSCHNEIDER, E. V. (1882-95): Botanicon sinicum. Jour. Royal Asiatic Soc. Gt. Brit. and Ireland. North China Br. New Ser. 16:18-230; 25:1-469; 29:1-623.

CARRIER, L. (1923): The beginnings of agriculture in America. McGraw-Hill, New York and London.

CIEZA DE LEÓN, P. DE (1554): La chronica del Peru, nuevamenta escrita (Pt. I.). M. Nucio, Anvers.

DORSEY, G. A. (1931): Man's own show; civilization. Harper, New York and London.

Egypt Exploration Soc. (1915-33): Theban tombs series (Editors: N. DE G. DAVIES and A. H. GARDINER). Egypt Exploration Fund, London.

HAWKS, E. (1928): Pioneers of plant study. The Sheldon Press, London; Macmillan, New York and Toronto.

KEMPTON, J. H. (1926): Maize and man. Jour. of Heredity 17:32-51.

LAURENT-TÄCKHOLM, V. (1932): Bibliographical notes to the flora of Egypt. Festskrift till VERNER SÖDERBERG, den fjärde Oktober, 1932. Kgl. Hovboktrykeriet Idums Tryckeri A.-B., Stockholm.

LEGGE, J. (1861-93): The Chinese classics. Trübner, London.

MANGELSDORF, P. C. and REEVES, R. G. (1939): The origin of Indian corn and its relatives. Texas Agr. Exp. Sta., Bull. 574.

MASPERO, H. (1927): The origins of the Chinese civilizations. Ann. Rept. Smiths. Inst. 433-452.

Papyrus Ebers (1931): The Papyrus Ebers, translated from the German version by CYRIL P. BRYAN. Appleton, New York.

SAFFORD, W. E. (1925): The potato of romance and reality. Jour. of Heredity 16:112-126, 175-184, 217-230.

SALAMAN, R. N. (1937): The potato in its early home and its introduction into Europe. Jour. Roy. Hort. Soc. 62:61-75, 112-123, 153-162, 253-266.

SARTON, G. (1934): The artificial fertilization of date-palms in the time of ASHUR-NASIR-PAL, B.C. 885-860. Isis 21:8-13.

STUART, G. A. (1911): Chinese Materia Medica; vegetable kingdom. American Presbyterian Press, Shanghai.

THOMPSON, R. C. (1924): The Assyrian herbal. Luzac and Co., London.

UNGER, F. (1857-59): Botanische Streifzüge auf dem Gebiete der Culturgeschichte. Gerold's Sohn, Wien.

WIGHT, W. F. (1916): Origin, introduction and primitive culture of the potato. Proc. Potato Assoc. of America, 3d ann. meeting, 35-52.

Chapter III.

THE NASCENT PERIOD.

The rise of natural philosophy:- The ethnobotanical period witnessed some notable advances in man's knowledge of the plant world, advances which were entirely empirical and characterized by the accumulation of information about plants. All the triumphs of discovery and domestication had been won by the trial and error process, as was the discovery of the art of roasting pork, according to the classical story of CHARLES LAMB.

The first attempts to understand the nature of the plant world generally ended in futile anthropomorphic fables or in deification of important plants. In general, man's knowledge of plants consisted of a mass of unrelated facts, principally gained, it is true, by experience, but totally unorganized so far as understanding any relationship was concerned. Slowly at first, but gradually accelerating, men began to search for rational explanations of natural phenomena, and this was a tremendous incentive to acquire additional knowledge about them. As more information was obtained theories could be extended or replaced by better theories. Continual verification was necessary, especially when, as always happens, theories were in opposition to each other. Therefore each activity helped the other forward. This process of verification and reconciliation has been one of the important tasks of science in all ages and is still important today.

Regardless of how this process got started, we know that it became a vital stirring force in the sixth century B.C. It is interesting to note that this eruption of intellectual activity happened not in one but in many countries; to wit, in Greece, in Palestine, in Babylonia, India, and China. It is remarkable how the human intellect has enjoyed these seasons of flowering at about the same time in many countries, situated at great distances from each other.

The Semitic mind was imbued with an idea of a divine immanence in the universe and was concerned more with understanding the nature of Deity than that of the Cosmos. It was, however, awake to the problem of man the finite in the presence of God the infinite, and necessarily, to that of the nature of man, as shown in many of the ancient Hebrew writings. The historical importance of Hebrew cosmogony upon European thought in medieval and modern times can never be disregarded.

Early Hebrew philosophy is pictured in the book of Job, which remains one of the great books of world literature. It was written by an unknown author in Palestine during the Persian domination of that country, or possibly at the beginning of the Greek period, the most plausible date is the fifth century B.C. SARTON emphasizes the unique scientific spirit which pervades the document. It is one of the great skeptical dramas of literature in which current beliefs were scrutinized and analysed in a way which reminds one of SHAKESPEARE and GOETHE. This unknown writer attempted

an explanation, not only of the Deity, but also of the Cosmos — a task which has occupied many another writer from that day to this. He expounded an idea of man and his place in the universe, setting man in the presence of the Infinite and showing that the whole is greater than any of its parts:

> Hast thou perceived the breadth of the earth? Declare if thou knowest it all. Where is the way where light dwelleth? And as for darkness, where is the place thereof that thou shouldest take it to the bound thereof, and that thou shouldest know the paths to the house thereof? Knowest thou it because thou wast then born, or because the number of thy days is great?

To a botanist the following passage is of interest:

> For there is hope of a tree, if it be cut down, that it will sprout again, and that the tender branch thereof will not cease. Though the root thereof wax old in the earth, and the stock thereof die in the ground; yet through the scent of water it will bud, and bring forth boughs like a plant.

Hebrew philosophy had little, if any, influence on Greece. At what time Egyptian geography and Babylonian astronomy and astrology reached Greece, it is impossible to say, because we have extremely fragmentary records of those times.

Greece was a young, vigorous nation, a frontier, if you like so to designate it, when the civilizations of Egypt and Babylonia had passed their apogee. Hardy individualists searching for more freedom in the less well-known northern regions had reached Greece and doubtless enjoyed the opportunity to impress new peoples with the traditional beliefs and sayings of their homeland. In Greece there was no formalized priest-culture, and thought was free to develop unhampered by the dogmas of a priesthood which reserved for itself all rights to higher learning and the prerogative of drawing conclusions. Religion in Greece never became a rational institution as in Egypt, Palestine and Assyria. In Greece religion was always primitive, even when social and political thought was well advanced. There was public instruction of a kind, not highly developed; in fact, rather rudimentary, since the youths had to learn only reading, writing, arithmetic, music and gymnastics. Beyond this stage the individual had to map out his own courses, usually choosing a school master to whom he went for more advanced studies. It thus happened that an unusual degree of academic freedom was achieved in Greece. It was a tradition that "the Greeks seek after wisdom".

In course of time a succession of men appeared in Greece who attempted to give some sort of rational explanation of the Cosmos. Unfortunately, we have only fragments of their writings and can obtain no adequate idea of what they wrote. Having neither the papyrus of the Egyptians nor the clay tablets of the Assyrians, they depended upon the perpetuation of the spoken word rather than upon complete written accounts of their ideas. It is certain, however, that they made some discoveries of fundamental importance in mathematics, astronomy, geography, physics, palaeontology, and medicine.

DEMOCRITUS OF ABDERA, born between 470 and 460 B.C., had a surprisingly modern point of view in science. Casting aside most of the former ideas of the origin of matter, he undertook to formulate a natural explanation of the structure and nature of matter. DEMOCRITUS adopted and further developed the idea of LEUCIPPUS

that the universe consists of a myriad of particles moving in empty space. He went beyond his predecessors by his more elaborate treatment of the philosophical doctrine of knowledge and is regarded as the founder of the atomic theory.

Few records of DEMOCRITUS' discoveries about plants remain, but he appears to have thought their diversities were due to the size and arrangements of the atoms of which they were composed. He said, according to THEOPHRASTUS, that the rapidly growing, short lived plants must have straight veins through which the sap and the winter cold could penetrate rapidly. NIKOLAOS DAMASKENOS grouped him with the philosophers who attributed intelligence and understanding to plants.

HIPPOCRATES, "The Father of Medicine" (born about 460 B.C.) is reputed to have been one of DEMOCRITUS' disciples. He lived to an advanced age, being famous as the founder of the Hippocratic school of medicine which started the study of the causes of disease. According to HIPPOCRATES and his school, four humors, blood, phlegm, yellow bile, and black bile, circulated in the human body; health depended upon the proper proportions of these humors. One is tempted to comment upon the scientific importance of the idea that disease is due to natural causes in an age when it was generally considered to have been of supernatural origin, but for the present, we must content ourselves with the knowledge that it cast new light upon the use of herbs. A list of about 240 plants used in medicine may be found in the writings of the Hippocratic school, but they were mentioned primarily for their medicinal properties, not being described botanically.

The Greek root-diggers (rhizotomoi) and drug merchants (pharmacopuloi), who engaged in the business of collecting and preparing drug plants, acquired knowledge which must have been advantageous. Their knowledge of plants was, however, empirical and full of superstitions and would have contributed little to the science of botany, without clarification by other students. That THEOPHRASTUS realized the limits of the knowledge of plants possessed by the root diggers and drug merchants is indicated by the following excerpt from the Enquiry into Plants, sect. 5:

> Further we may add statements made by druggists and herb-dealers, which in some cases may be to the point, but in others contain exaggerations. Thus they enjoin that in cutting some roots one should stand to windward, - for instance in cutting *Thapsia*, among others, and that one should first anoint oneself with oil, for that ones body will swell up if one stands the other way. Also that the fruit of the wild rose must be gathered standing to the windward, since otherwise there is danger to the eyes. Also that some roots should be gathered at night, others by day, and some before the sun strikes on them, for instance, those of the plant called honey-suckle.

Although the people of that day were unaware of it, science turned a corner in the fourth century B.C. Things were studied, compared, dissected, analysed as a basis for rational ideas about their essential characters. The development of biology as a science began with the work of ARISTOTLE and THEOPHRASTUS in Greece.

ARISTOTLE, the Stagirite:- The prodigious activity of ARISTOTLE (384-323 B.C.) marks the climax of the Golden Age of Greece. The very existence of his works proves not simply that he had an encyclopedic mind of the highest order, but also that a large

amount of scientific research had been accomplished by his predecessors. His deep mathematical knowledge was happily balanced by a very extensive acquaintance with every branch of natural history. There is a marked difference between ARISTOTLE and his teacher, PLATO, who had tried to set up a unitary ideal to adumbrate the infinite and unsearchable. ARISTOTLE's philosophic system was more closely allied to what we call the scientific point of view. He was untiring in his search for facts, fertile in explanations which are marked by practical good sense, and based on historical and scientific considerations. He combined in himself, as few other philosophers have done, scientific and metaphysical interests.

For scope of interest and profundity of learning, ARISTOTLE has no equal. His ideas pervaded the western world for hundreds of years. VOLTAIRE tells us that two years after KEPLER published his *De Motibus Stellae Martis*, and in the year of GALILEO's observations of the moons of Jupiter, the Parliament of Paris passed a law to make chemists conform to the teaching of ARISTOTLE under pain of death and confiscation of goods.

ARISTOTLE was born in 384 B.C., the son of NICOMACHUS, physician to the royal family of Macedonia. Born in Stagira, a small Greek colony on the Macedonian coast, he was sometimes called the Stagirite. His father, NICOMACHUS, was a member of the guild of the Asclepiads which was composed of physicians using herbs and other remedies known only to members of the guild. At seventeen ARISTOTLE went to Athens where he met and became a pupil of PLATO. The institution where PLATO taught, known as the *Academy*, was simply a grove of trees where the Teacher and his pupils were wont to assemble. ARISTOTLE, though essentially a biologist, was closely attached to his master and continued to be a member of his school until PLATO's death in 347 B.C. ARISTOTLE perhaps expected to become head of the Academy. In this, however, he was disappointed and left Athens to reside at the court of a sovereign of a small Greek state on the coast of Asia Minor opposite the island of Lesbos. Here ARISTOTLE's bias toward natural history had full play. He enjoyed ample leisure and good opportunities for investigating marine animals. The results of his investigations at Lesbos frequently come out in his biological treatises.

In the year 342 B.C. ARISTOTLE received an invitation from King PHILIP of Macedon to become the tutor of his son ALEXANDER. He accepted and settled in Macedon, where he remained seven years. ALEXANDER owed much to the training received from the great biologist, if we may judge from certain of his later interests. In the year 336 PHILIP was assassinated, ALEXANDER succeeded to the throne, and ARISTOTLE returned to Athens.

When ARISTOTLE returned to Athens, he opened a school of his own instead of returning to the Academy. He established his school in the walks of the Lyceum where he lectured. According to tradition he gave two kinds of instruction; in the morning he taught to a rather small circle of advanced pupils his esoteric doctrine, in the evening he expounded his exoteric teaching in the form of more popular lectures to a larger audience. Of the equipment of the school in books and material, we know nothing.

After the death of ALEXANDER (323 B.C.) the party opposed to Macedon seized power in Athens and ARISTOTLE felt constrained to withdraw from Athens.

ARISTOTLE founded the first botanical garden of which there is any reliable record. A number of his biological works have survived, and, fortunately, are in a fairly good state of preservation. Four are major treatises, and there are a number of less importance. The major works are most frequently referred to by their titles translated into Latin.

(a) On psyche (De anima)
(b) Histories about animals (Historia animalium)
(c) On the generation of animals (De generatione animalium)
(d) Of the parts of animals (De partibus animalium)

These treatises contain not only his own knowledge but also a compendium of all that had been learned by his predecessors. They were intended to become a part of his cyclopedic cosmic theory, a scheme which has been the admiration of the students of the succeeding centuries.

On psyche deals with what we may call the living principle, quality, nature, essence, or whatever we may call it, that distinguishes living substance. This quality, nature, or essence departs, ceases to exist, or to act when living substance dies. Various interpretations have been placed on Aristotle's ideas, but he is regarded as the founder of the theory of vitalism, which dominated biological science for centuries. ARISTOTLE reached the conclusion that there were different kinds or orders of psyche or soul. He was led to differentiate between a vegetative, an animal, and a rational soul.

The vegetative soul is shown by plants, which exhibit the phenomena of nutrition, growth, and reproduction.

The animal soul is higher than the vegetative, while animals have the properties of plants, they also have sensation and the power of movement.

The highest soul is that found in man, who exhibits all the qualities of the lower forms of life, and certain others. He reasons and his movements and actions are directed by his thoughts. He is therefore equipped, according to ARISTOTLE, not only with a vegetative and an animal soul, but also with a rational or an intellectual soul.

Only fragments remain of ARISTOTLE's botanical writings. Unfortunately, his five books, cited by himself on the theory of plants, are among the lost works. What little we have is derived from incidental statements scattered through his other writings.

ARISTOTLE ascribed the longevity of trees to their low water content. Herbaceous plants, being succulent, are short lived because their moisture is readily congealed in winter. He was not content, however, with this apparently simple explanation of longevity. He believed that the property of growth and regeneration explained much that had puzzled him. Noting that destruction of the trunk and branches is often followed by an upsprouting of new shoots from the stump, and that new roots grow from the older roots, he learned that the life of the tree continues, "part dying and part being born". He concluded that the vital principle exists potentially in every part, since even a slip can reproduce the whole plant. The nutrition of organisms appears to have given him a knotty problem to solve, and he was obliged to resort to dialectic

and metaphysic in place of experiment. He realized that nutritive function clearly separates the living from the dead:

> There is a general opinion that opposites are nutriment to opposites; not of course in every case, but among such opposites as have not merely their birth from each other, but their growth as well; for many things arise from each other, but they are not all quantities; for instance, health from illness. (De anima Book II, chapter 4).

Observing that there is a vital principle which maintains the hereditary properties of an organism, he concluded that the food prepares it for its work, therefore it cannot continue to exist when deprived of food. His discussion of nutrition leaves us mystified and unsatisfied, but we are certain that he visualized the problem. He commented on the fact that green is the characteristic color of plants, although, naturally he had no real explanation of it, nor even approached the significance of chlorophyll.

The plant was an integrated thing to ARISTOTLE; leaves, shoots and roots were not merely appendages of the plant but were members of an organized thing. Each of them had its own characteristics but they had dependencies, relations, and harmonies which interacted to maintain the life of the whole.

Theophrastus of Eresus:- Botanical science in its broadest aspects received a tremendous stimulus in Greece under the leadership of THEOPHRASTUS and his disciples. He was the founder of botanical science and one of the greatest botanists of all time. In his ability to collect information, to make careful observations, and to reason from cause to effect he is comparable to his great teacher, ARISTOTLE. THEOPHRASTUS was born, ca. 371 B.C. in Eresus on the island of Lesbos. He first attended the school of a philosopher in his native city, but went to Athens as soon as possible and studied in the Academy until PLATO's death, 347 B.C., then, while still a young man, he joined himself to ARISTOTLE. This was the time when, as previously stated, ARISTOTLE left Athens to live at the court of a small Greek state on the coast of Asia Minor opposite the island of Lesbos, near Eresus, the birthplace of THEOPHRASTUS. It is quite possible, although proofs are lacking, that the disciple followed his master thither. In Stagira, where THEOPHRASTUS probably sat with the youthful ALEXANDER listening to the lectures of ARISTOTLE, he owned a landed estate which he bequeathed to DIOGENES LAËRTIOS, according to his last will and testament. Who can say what influence this discipleship had both on the relations of THEOPHRASTUS to ARISTOTLE and on the whole organization of botany? Be that as it may, until ARISTOTLE finally left Athens in 322 B.C. THEOPHRASTUS was never separated from him again.

There is evidence that ARISTOTLE had the greatest esteem for THEOPHRASTUS. Traditionally the original name of the latter was TYRTAMOS, but ARISTOTLE soon gave him the name EUPHRASTOS, the Eloquent, to be replaced later with THEOPHRASTUS, the Divine spokesman. A more reliable indication of ARISTOTLE's esteem consists of his will by which he made THEOPHRASTUS his legatee and gave him the Lyceum with its garden and his library which was the largest which had ever been assembled. THEOPHRASTUS took ARISTOTLE's son under his particular care after his father's death.

THEOPHRASTUS is said to have had 2000 disciples and to have written more than 200 treatises, of which his two botanical works "The history of plants" and "The causes of plants" are the most important that have survived. Many of his observations were made in the garden of the Lyceum, but his knowledge, by no means confined to the plants of Greece and Asia Minor, included many plants brought from Asia by ALEXANDER's followers. It is even possible that he sent out trained observers to explore and report on the plants of remote places. The style of his books suggests that, as in the case of ARISTOTLE, what we possess consists of notes for lectures, or notes taken of lectures. There is no literary charm; the sentences are for the most part compressed and highly elliptical, to the point sometimes of obscurity.

THEOPHRASTUS' writings showed that he had acquired a great store of knowledge about plants in addition to all that which ARISTOTLE had attained in his brief day.

> He wrote from the midst of an advanced civilization; a state of society in which there was much farming, extensive cultivation of the vine and olive, fruit growing, market gardening, and cultivation of medicinal, aromatic, and ornamentally flowering shrubs, herbs, and trees; a time when many cultivated varieties of all sorts of things had been derived through cultivation, and when it was perfectly well known that such improved varieties can not be depended on to come true to seed, but may be preserved, and the stock of each increased by division of roots, by cuttings, and by grafting. (GREENE, Landmarks of botanical history).

Outstanding is THEOPHRASTUS' way of organizing his knowledge, placing parts in their relation to each other, and to the whole plant. In this task he went far beyond ARISTOTLE. Whether he learned the principle of classification from PLATO or from ARISTOTLE, he appears to have been the first to apply it systematically to plants. He classified them as trees, shrubs, and herbs, thus originating a system which endured for 2000 years. When he discovered the forms and functions of the plant organs he was remarkably free from the errors of his predecessors, who tried to harmonize everything in the plant with the form and functions of animals.

At the outset THEOPHRASTUS grappled with the problem of classification, realizing that there must be a principle, or set of principles, according to which he could make an orderly arrangement of what he saw in plants. He said, "In considering the distinctive characters of plants and their nature generally one must take into account their parts, their qualities, the ways in which their life originates, and the course which it follows in each case; (conduct and activities we do not find in them, as we do in animals)". THEOPHRASTUS had a peculiar genius for classification. Throughout his botanical works the constant implied questions are: "What is its difference?" and "What are the characteristic features in virtue of which a plant may be distinguished from other plants, and which make up its own *nature*, or essential character?" For example, in Book I of the Enquiry into Plants he says:

> Wherefore the differences between plants must be observed in these particulars, since taken together they show forth the general character of each plant. But, before we attempt to speak about each, we must make a list of the parts themselves. Now the primary and most important parts, which

are also common to most, are these — root, stem, branch, twig; these are the parts into which we might divide the plant, regarding them as members, corresponding to the members of animals; for each of these is distinct in character from the rest, and all together they make up the whole.

THEOPHRASTUS proceeded cautiously in defining plant organs, preferring physiological to morphological characteristics. He said the root is that by which nourishment is taken up, - a safe definition, but not very satisfactory to modern botanists who demand morphological distinctions. It was a definition which he originated and which he intended should displace one which merely stated that the root was the underground part of the plant. The roots of herbaceous growths he classified as ligneous, fibrous, and fleshy; and these included many things recognized in modern botany as subterranean stems, that is bulbs, corms, tubers, and the more thick and fleshy forms of root-stock, or rhizome. Although tempted to criticize him for these mistakes, we should remember that for two thousand years and more botanists accepted the definition of THEOPHRASTUS.

He designated the stem of a plant primarily as the main vehicle of nourishment to the other parts; adding that it rises up singly from the ground. This was to distinguish it from the branches and leaf stalks, both of which were known to him to be channels also for aliment. This definition, equally with that of the root, evinces his distrust of morphological characteristics as definitive, and his feeling that the physiological ones are safer. He did not attempt to characterize the leaf morphologically, or even physiologically, for he could not with any degree of certainty name its chief function. So, without vouchsafing any definition of it, he merely described its many aspects.

Leaves are commonly attached to the stem or branch or whatever else supports them by a stalklet; this either firm and holding the leaf steadily in a certain position, or else slender and feeble, allowing the leaf to hang downward and perhaps tremble with the passing breeze, or even to become inverted, turning the usually paler lower face upward. But there are also leaves with no stalklet, these adhering directly to the branch. Some leaves arrange themselves only in opposite pairs, with regular intervals between the pairs, while others are scattered singly and without order up and down the stem. (GREENE, Landmarks of botanical history).

THEOPHRASTUS' perspicacity never showed to better advantage than in his descriptions of the mode of germination and the subsequent development of the seedlings. He emphasized the fact that wheat and barley come up with a single leaf (monophyllous plants), but that peas, beans, and chick-peas have several leaves (polyphyllous plants). He also recognized the unbranched stems and parallel leaf-veins of the plants now called Monocotyledons as distinct from the branched stems and netted leaf-veins of the Dicotyledons. It is remarkable that this fundamental distinction was overlooked for so many centuries by botanists. He distinguished the types of root and shoot development of the two saying that the leguminous plants have a single woody root from which delicate side roots arise, but wheat and barley and other cereals have a number of fine roots wherefore they are matted together. The leguminous plants, except beans, have many side growths above from the stem, while the cereals, which have many roots, send up many straight shoots.

The system of plant classification which THEOPHRASTUS evolved was largely based on the characters of the leaf. For him and for others it is an obvious and useful character and has been followed from his time to the present. Accordingly, we find such specific names as, *salicifolia, malvaefolia, cordifolia, rotundifolia,* and the like.

A nomenclature of some sort existed in THEOPHRASTUS' day, in fact had long been recognized by root-diggers, wood-cutters, charcoal-burners, and farmers. If a genus consisted of several kinds of plants, each was designated by a second name, being what we would call the species name; for example, white oak, silver fir date palm, and the like. THEOPHRASTUS gathered and codified the names of nearly 500 plants so that the names obtained general recognition, in fact, some of the names are used in the modern system of nomenclature.

THEOPHRASTUS recognized ecological groups of wild plants, emphasizing the differences between habitats.

> Others affect only marshes or other very wet places. Some cannot live in very wet ground, but restrict themselves to dry ground. Certain others are littoral only. A few trees thrive in either moist land or dry; such are the myrtle, alder, and willow.

He also points out that there are trees, peculiar to mountain districts, and others confined to lowlands and plains, as indigenous in the former habitat the fir, wild pine, spruce, holly, box, walnut, chestnut, and many more are mentioned. Other kinds grow only on the plains; among them are elm, ash, maple, willow, alder, and poplar; while a few kinds of trees are common to both mountain and plain. In the mountains some trees like the wild pine, for example, thrive on slopes that look southward and will hardly grow at all in other places, while others on the contrary, among them the fir, attain perfection on the cool and shady sides, and if ever seen elsewhere, have an inferior growth and is unlike itself. As a general rule the kinds of trees growing in cool and shady places are tall and straight, their trunks not forking or parting into subsidiary or trunk-like branches; but he noted that arboreal growths of this latter description are found in open and sunny places. Certain trees are wont to grow nowhere but along water-courses and certain others belong exclusively to the highest elevations of the mountains near perpetual snow.

De Causis Plantarum contains less of scientific interest than the Historia, but carries on the inquiry in a philosophical spirit. The subjects discussed are (1) propagation of plants by seeds, grafting, and budding; (2) the effects of weather and soil; (3) the arts of cultivation; (4) growth and periodicity in plants; (5) heat and cold in plants.

THEOPHRASTUS was a pretty orthodox vitalist, in harmony with his teacher ARISTOTLE. Although soil, light, heat, etc., may affect the growth and fruit production of plants, there is still an innate factor which is independent of the external factors. Discussing the periodicity of growth, he said:

> Perhaps this question is a general one and concerns also the other parts of the plant. For though every living thing is nourished, growth will result only when it is nourished by the impetus for germination; now, all plants,

everywhere, old as well as young, feel the urge for growth . . . For the branches, whether large or small, have within themselves certain vital principles, which when they are warmed up in spring, send forth buds even though the plants be not rooted below. This is most readily seen in the slips taken from vines and other plants and set in pots; for as soon as the season comes on, the buds open up before the leaves grow . . . This would indicate that such plants are already in possession of the vital elements and capacities.

THEOPHRASTUS was not so far removed from the atmosphere of supernatural ideas that he could escape belief in spontaneous generation. After discussing the ways by which plants may be reproduced, he said:

Spontaneous generation takes place in smaller plants, especially in those that are annuals and herbaceous. But it still occasionally occurs too in larger plants whenever there is rainy weather or some peculiar condition of air or soil; for thus it is said that silphium sprang up in Libya when a murky and heavy sort of wet weather condition occurred, and that the timber growth which is now there has come from some similar reason or other; for it was not there in former times.

Just to show that there was another side to the question, he put forth observations about the dissemination of small seeds and the transport of seeds by rivers, "Wherefore also, changes in the courses of rivers make many places wooded that before were woodless".

Space does not permit speaking further of the scientific advances which THEOPHRASTUS made. Perhaps enough has been said to establish his right to the title "Father of Botany". His life must have been a remarkable experience; he studied under PLATO and ARISTOTLE, witnessed the careers of PHILIP and ALEXANDER of Macedon, and knew the latter personally. He died about 285 B.C., having remarked, "We die just when we are beginning to live".

The Ptolemaic school at Alexandria:- When Greece lost her liberty after the dissolution of the Alexandrian empire, she lost also her scientific originality. From the time of ALEXANDER to that of AUGUSTUS, the great city of Alexandria became the center of Greek intellectual activity, where, for a few centuries, conditions for scientific development were extremely favorable. The result was an assemblage of men having genuine scientific talent. In the wealth of its endowments the "Museum", or college and library, founded in the Egyptian capital by the first PTOLEMY, offered unrivalled attractions to learned men.

PTOLEMY I (c. 367-283 B.C.) surnamed *Soter* ("the Preserver") was a Macedonian having marked ability as a soldier. He was one of ALEXANDER the Great's favorite generals in his eastern campaigns. On the death of ALEXANDER (323 B.C.) and the subsequent division of his realm, Egypt and Libya fell to the share of PTOLEMY. While nominally only a satrap of these provinces, he was from the first virtually an independent ruler. In 306 B.C. he became King in name as well as in fact.

The transplanted Greek culture mingled with new aspirations gathered from Egyptian and other sources, and assumed an analytic, rather than synthetic approach to problems of the natural world. Men like EUCLID and HEROPHILUS, ARCHIMEDES and APOLLONIUS turned from the methods of PLATO and ARISTOTLE feeling

that enough had been done in the way of philosophic synthesis and that the time had come for a new method of attack on the individual problems of science by the combined efforts of specialists who had the merit of having invented some of the new methods of investigating nature.

Perhaps the ball would not have started to roll so fast without the kick given to it by PYRRHO (360-270 B.C.) who is remembered for his deep-rooted skepticism. He maintained that no knowledge of things is really possible and averred that man can know nothing nor prove anything, — neither the possibility of knowledge nor the justification of doubt. This iconoclastic principle naturally precluded any philosophy of nature, but it was just the thing which drove the philosophers to devote themselves to special studies on definite scientific subjects and the Alexandrian medical school advanced the science of biology.

HEROPHILUS (ca. 300 B.C.) a teacher and investigator in Alexandria, was one of the greatest anatomists of antiquity, but his writings were lost. He was especially famous for discoveries in human anatomy. Skeptics as they were, he and his pupils despised the traditional fear of dissecting human bodies, and the enlightened Ptolemaic rulers placed material at their disposal. HEROPHILUS, according to report, carried out investigations on living human beings — criminals condemned to death — whose internal organs he studied in the living state. He investigated the circulatory system; the walls of the arteries and veins; compared the pulse at different ages and under different bodily conditions.

In the province of botany no real advancement was made at that time in Alexandria.

General interest in the development of science requires mention of EUCLID (323-285 B.C.), the eminent mathematician who taught and founded a school of mathematics at Alexandria in the time of PTOLEMY I. He was essentially a systematizer and compiler. His 13 books of the Elements of Geometry have remained to our day the basis of the teaching of that subject. They were partly original and partly compiled.

The decline of Greek learning:- The scholarly work of the Ptolemaic school was eventually seriously impaired and lost its vitality, due in part to clashes between rival teachers and also to the lack of support by the later Ptolemaic kings. The degraded natures of those who ruled and oppressed their subjects would not encourage such noble pursuits as those of scholars. The finishing blow to scholarship was given by the fanatical Christian Church in Egypt.

In the mother country the Greeks also forgot how to study things objectively and to draw logical conclusions from what they learned. A fog of mysticism overspread the intellects of men. In contrast to the objectivity of THEOPHRASTUS in studying plants, a decline of interest in natural philosophy followed and a mounting interest in sorcery, magic, poison-antidotes, love-philtres and the like.

Greco-Roman writers:- The Romans being a practical people, held agriculture in the highest esteem. MARCUS PORCIUS CATO was born at Tusculum in 234 and died at Rome in 149 B.C. While Roman armies were waging the Punic wars, CATO, surnamed

"The Censor", wrote his *De Re Rustica,* which ranks well in the field of Roman literature. It was the first agricultural book written in Latin. Our interest centers in the list of 120 plants which he mentions, including the varieties and certain imported plant products handled by the apothecaries. CATO had no sense of necessity for classifying plants, except in connection with the business of farming, gardening, and fruit growing. His list of plants lacks organization and names were sometimes repeated.

COLUMELLA, VARRO, and VERGIL subsequently wrote in like manner on agricultural matters, but their works show little of the scientific spirit of inquiry which characterized the Greeks.

The second half of the first century A.D. was a time of revival. A sharp recrudescence of intellectual energy can be witnessed in almost every field. Geographical horizons were enlarged; London was established as a Roman settlement; AGRICOLA sailed for the first time around Britain; an ocean route to India was opened up through the Red Sea; wealth increased. Into this world which bristled with opportunities for assembling and collating multitudes of new discoveries, CAIUS PLINIUS SECUNDUS, known as PLINY the Elder, was born at Como in 23 A.D. and died while observing the eruption of Vesuvius in 79. Historians have frequently commented upon PLINY's extraordinary capacity for work and described the way in which he continuously studied, read, or dictated to his secretaries. Since the circumstances attending his death throw so much light on the man, it will be worth while to mention them. While with the fleet at Misenum (modern Miseno), he saw the great cloud rising from the crater of Vesuvius and taking the shape of an Italian pine tree. He went at once to the shore near Pompeii, observing and dictating notes on the phenomenon to a secretary. Despite a surging sea beneath and a shower of hot ashes and pumice from above, PLINY continued his way to the shore. Having landed he consoled his friend who had called for help, bidding him calm his fears, and asked to be conducted to his bath. In spite of the eruptions and of the terrors of the inhabitants PLINY went calmly to sleep. Eventually the earthquakes and the fall of red-hot cinders were so dangerous that it was decided best to flee to the shore where an angry sea was surging. PLINY was induced to lie on the ground on a rug spread for him, where he was eventually killed by sulfurous fumes. When he was found later he was whole and uninjured, appearing as though he were asleep.

PLINY's "Natural History" in 37 books is a very elaborate encyclopedia, often uncritical, but of great value, since it contains a wealth of information not to be found elsewhere. He said it was compiled from some 2000 volumes, most of which have since been lost. It had a profound influence on the students of biological problems from the time of the Roman Empire through the Middle Ages and almost to the dawn of the 19th century. During the Middle Ages most writers were content to copy PLINY, errors and all. It was the foundation of the encyclopedias of BARTHOLOMAEUS ANGLICUS, KONRAD OF MEGENBERG and others. PLINY had visited Africa, Egypt, and Greece, served in the army in Germany and reached the shores of the North Sea in Belgium. He collected information wherever he found it. His principal authorities were undoubtedly Greek; ARISTOTLE and THEOPHRASTUS were frequently mentioned. Despite errors which we are obliged to admit, viewed

as a naturalist, PLINY was one of the most meritorious of the Roman writers.

Plants occupy the attention of 16 of the 37 books; descriptions of trees fill four books, agricultural subjects three and medicinal properties of plants the remainder.

The following extracts will give the reader an idea of his lucid style and his attention to details:

> The acorn of the beech is similar in appearance to a kernel, enclosed in a shell of triangular shape. The leaf is thin and one of the very lightest, is similar in appearance to that of the poplar, and turns yellow with remarkable rapidity. From the middle of the leaf and upon the upper side of it, there mostly shoots a little green berry, with a pointed top (one of the galls produced by oviposition of an insect). The beech is particularly agreeable to rats and mice; and hence it is, that where this tree abounds, those creatures are sure to be plentiful also. The leaves also are very fattening for dormice, and good for thrushes too. Almost all the trees bear an average crop but once in two years; this is the case with the beech more particularly. (Book 16, chapter 7).
>
> The other trees that bear acorns, properly so-called, are the robur, the aesculus, the cerrus, the holm-oak, and the cork-tree: it is contained in a rivelled calyx, which embraces more or less of it, according to the several varieties. The leaves of these trees, those of the holm-oak excepted, are weighty, pulpy, long, and jagged at the edges, and they do not turn yellow before they fall, as with the beech; they are also longer or shorter, as the case may be. (Book 16, Chapter 8).

PLINY seemed to have little interest in the classification of plants on the basis of their resemblances. He classified trees as forest trees, exotic trees, and fruit trees. He divided the forest trees into glandiferous and pitch-bearing; the former including all the catkin bearing trees, the latter most of the *Coniferae*.

From 79 A.D. to 1469, PLINY's work existed in manuscript. During the Dark and Middle Ages, however, the esteem for the *Historia* was so great that copies were made in great numbers, as shown by the fact that some 200 manuscripts are known today. When the new learning started in Europe it was necessary to purge the copies of errors which had crept in. Its prestige during the Middle Ages was no doubt due in part to the fact that it was written in Latin which was the language of the scholars of the time.

DIOSCORIDES, a Cilician Greek, who lived in the first century A.D. was the most important botanist after THEOPHRASTUS. His principal writings were on medical botany. During the Middle Ages his work was far more popular than that of THEOPHRASTUS though he knew less about botany. For more than 1500 years he was the alpha and omega of European botany.

PEDANIOS DIOSCORIDES was a native of the city Anazarbos in Cilicia. There is some doubt about the time when he lived, but it seems safe to assume that it was in the first century A.D. He was a learned physician, had travelled extensively to study plants, and had obtained knowledge of remedies obtained from sources other than plants. He acquired so much information about plants new and old that he was impelled to make descriptions not only of their pharmaceutical properties, but also of their habit of growth and form. Therefore he described their roots, stems, leaves, and sometimes their flowers — always the entire plant, not a fragment. The number described was about 600, no small task.

He gave the vernacular names of the plants, but often supplemented them with the Latin, Punic, Egyptian, Dacian, and Gallic synonyms. He made no genuine classification, grouping plants merely as aromatic, culinary, and medicinal kinds, though there is evidence that he knew more about the matter than we suspect. At any rate, he did not follow the plan of his illustrious predecessors of grouping plants as trees, shrubs, and herbs. For example, some aromatics are trees, others shrubs, and still others herbs. The same is obviously true of culinary, and of medicinal plants. He arranged plants with labiate flowers in one series, those with leguminous flowers in another, and those with umbelliferous flowers in still another.

The pictures of the plants, as well as descriptions, gives the herbal even greater importance than any previous work on plants. So far as we know it was the first illustrated herbal, though there had been many plants represented on buildings and in tombs of the Assyrians and Egyptians. It is not difficult therefore to understand why DIOSCORIDES' herbal has been more attentively studied word for word and line by line than any other book on botany which has yet been written, unless we should be obliged to make an exception of BAUHIN's Pinax. During the Middle Ages no drug plant was considered genuine unless it could be identified by DIOSCORIDES' description.

As students of classical botany, we cannot fail to be interested in the history of the manuscripts of DIOSCORIDES' herbal. Although written in Greek, it was translated at an early date into Latin. For many centuries Latin versions continued to appear, since that was the universal language of the schools. The earliest and most beautiful is the Byzantine MS. known as the Codex Aniciae Julianae, prepared for the Princess ANICIA JULIANA, the daughter of FLAVIUS ANICIUS OLYBRIUS, who was emperor for part of the year 472. The Princess ANICIA JULIANA died in 527. About the year 1562 this MS. was purchased by the Holy Roman Emperor and brought to Vienna; at the instigation of PIER'ANDREA MATTHIOLI.

The parchment MS. was sumptuously reproduced in photogravure in 1906 and published in two large folio volumes by SIJTHOFF under the direction of DE VRIES, prefect of the university of Leiden. It shows that the original pages are dog-eared, their margins notch and fissured, yet the illustrations of plants are clear. Many a scribe has annotated them in Greek and Arabic. The pictures look as though the plants had been flattened by pressure, and a strong tendency to conventionalize them is apparent. There was an attempt to show the roots as well as the stems, since the physicians believed that the greatest concentration of medicinal qualities was in the root. Flowers were generally, but not universally, depicted.

DIOSCORIDES' work is also of importance for the study of ancient chemistry, as it describes simple chemical preparations (for example), to obtain mercury from cinnabar, or potash from tartar, mentions the earliest reactions of wet analysis, the detection of iron vitriol by means of gall-nut juice, and quotes many chemical substances.

There is need for but a word about ancient science. The attempt to discover a rational explanation of the world was supreme in

the minds of the men who made this period of the rise of natural philosophy one of the greatest intellectual epochs of all time. Men began to think originally and fundamentally about the universe, supernaturalism and mythology were abandoned in preference for logic. During this time the foundations for scientific study of nature were laid, and although the building was long neglected, the foundations were found when the intellectual rubbish was eventually removed.

REFERENCES:

DIOSCORIDES (1934): The Greek herbal of DIOSCORIDES; illus. by a Byzantine, A.D. 512; Englished by JOHN GOODYER, A.D. 1655; ed. and first printed, A.D. 1934, by ROBERT T. GUNTHER. Oxford University Press, Oxford.

GREENE, E. L. (1909): Landmarks of botanical history. Part I - Prior to 1562 A.D. Smithsonian Institution. Smithsonian miscellaneous collections, Part of vol. 54, Publication 1870.

HAWKS, E. (1928): Pioneers of plant study. Sheldon Press, London; Macmillan, New York and Toronto.

NORDENSKIÖLD, E. (1928): The history of biology (Transl. from the Swedish by L. B. EYRE). Knopf, New York and London.

SARTON, G. (1927): Introduction to the history of science, Vol. 1. (Carnegie Institution of Washington, Pub. no. 376).

STRÖMBERG, R. (1938): Theophrastea. Handlingar Göteborgs k. vetenskaps- och vitterhets-samhälle, 5. följden, Ser. A, Bd. 6, No. 4, 1-234.

THEOPHRASTUS (1916): Enquiry into plants . . . with an English transl. by Sir ARTHUR HORT, bart. Heinemann, London; Putnam, New York.

——— (1927): De causis plantarum. Book one. Text, critical apparatus, translation, and commentary, by R. E. DENGLER. Thesis (Ph.D.) Univ. of Pa.

Chapter IV.

THE RETROGRESSIVE PERIOD.

It will evoke no surprise to find that the scientific study of plants fell into abeyance about the beginning of the third century, when all other channels of progress for intellectual streams were closing. When freedom vanished, when superstition superseded science, and profligacy displaced industry, the progress of science was stopped. The scope of this book will not permit an analysis of what some of the most eminent scholars in the world have critically and thoroughly described as the eclipse of the human spirit in those centuries.

Seeking to preserve the empire, the Romans stifled agriculture and other arts. They built roads to the provinces instead of making improvements in agriculture. Over those roads they transported the foods which their tax-collectors squeezed out of the tribes of the conquered lands, and over the roads they sent armed forces to liquidate any tribes which were inclined to be ungenerous with their goods. In their minds, this was the way to stabilize the empire. Roman Science, if it can be called such, was concerned only with practical affairs. This exclusively empirical concern is one of the signs of a dying science. The bad government of the north European colonies caused a decline and eventual abandonment of many of the farms. Natural resources were wasted.

For a time the extension of trade routes promoted the development of geography and, very incidentally, the knowledge of exotic plants and animals. Roman trade routes penetrated far into central Africa and eastward across Mesopotamia and Iran to India and China. The routes and means of intercommunication were highly developed as the few itineraries which have been found clearly indicate. In 1923 CUMONT found at Salihiyeh on the Euphrates a fragment of the shield of a Roman soldier bearing a list of the army's stopping places. The caravan route by which silks and other products were carried from China to Rome was mentioned by several Chinese writers of the third century, but no valuable work on geography or natural history was written.

GARGILIUS MARTIALIS is one of the few writers of this period about whom we have any information, scanty though it is. His works on the medical properties of fruits and herbs were subsequently prized in Europe, for, although he did nothing original, his writings were free from the superstitions prevalent among the writers of his day. What he said was in the tone of a scientist and based on sound botanical principles. The fragmentary knowledge we possess of his writing is derived from a manuscript found in 1826 in the Royal library in Naples, and from one found in the Vatican library. He devotes four chapters to a discussion of plants, *viz.*, quince, peach, almond, and chestnut.

APICIUS COELIUS was the pseudonym of a whimsical gourmet who wrote a diverting cook book in the third century. MEYER says that no writer of ancient or medieval times knew this man or his work. The manuscript was found in 1454 and acquired for the Vatican library. The man appears to have been something of a wag, but the names of the plants which were utilized in one form or another in the cuisine of his day are of some interest. His work, moreover, is the first comprehensive cook-book of the western world. Concerning the name "Apicius" there is no little confusion. GOLLMER mentions that of four men who have come down in Roman literature, only three can be definitely connected with it. All of them were, according to the standards of the time, great gourmands or gourmets.

According to some writers, only MARCUS COELIUS APICIUS, who was also known as MARCUS COELIUS should be considered as the author of the famous book. That is, however, by no means certain, for the uncertainty of the earliest writers leads one to believe that the proper name of this one was allowed to be lost and the name of APICIUS substituted, since he was concerned with a work on the art of cooking. This would be worthy of note, because we know that the old Romans were accustomed to designate choice and coveted foods with the name "Apicius". For us, however, it is quite certain that all of the previous writings given out appeared under the name of COELIUS APICIUS.

The important point is that some empirical writer on cooking definitely knew a respectable list of plants and that he recorded their names. Native and important plants were included. It shows that these names were so generally known by the folk of that day that the plants could be readily distinguished by anyone who could read. Possibly this was the result of the reading of CATO and other agricultural writers.

The first half of the fifth century was a time when barbarians were invading and plundering a decadent Rome, but *per contra* much culture from the Mediterranean region seeped into the interior of Europe. One of the important agencies in this diffusion of south European ideas was the activity of Christian missionaries who penetrated the uncivilized northern countries, carrying with them some of the Roman civilization, often, the innate jealousy and doctrinal strife of the theologians were the driving forces which sent the non-conforming members to new fields.

In one of the provinces of the Roman Empire a new book on remedies was written in 410. The author, MARCELLUS EMPIRICUS, of Bordeaux, not a physician according to his own statement, appears to have acquired considerable knowledge of the region in which he lived, and wrote his treatise De medicamentis in the form of a letter to his sons. As a piece of medical literature his writing was comparatively worthless, but it has much of botanical interest in it. MEYER said:

> After PLINY, I know of no other writer until MARCELLUS, who described more plants; and he wrote, not for the learned, but for his Celtic compatriots. And as he says, he drew his information, not from the writings of his predecessors, but from the mouths of the common people. So we may regard his as the rudiments of a *Flora Gallica.*

PSEUDO-APULEIUS wrote an herbal which is dated in the fourth century. Of the real author we know little since he hid behind the

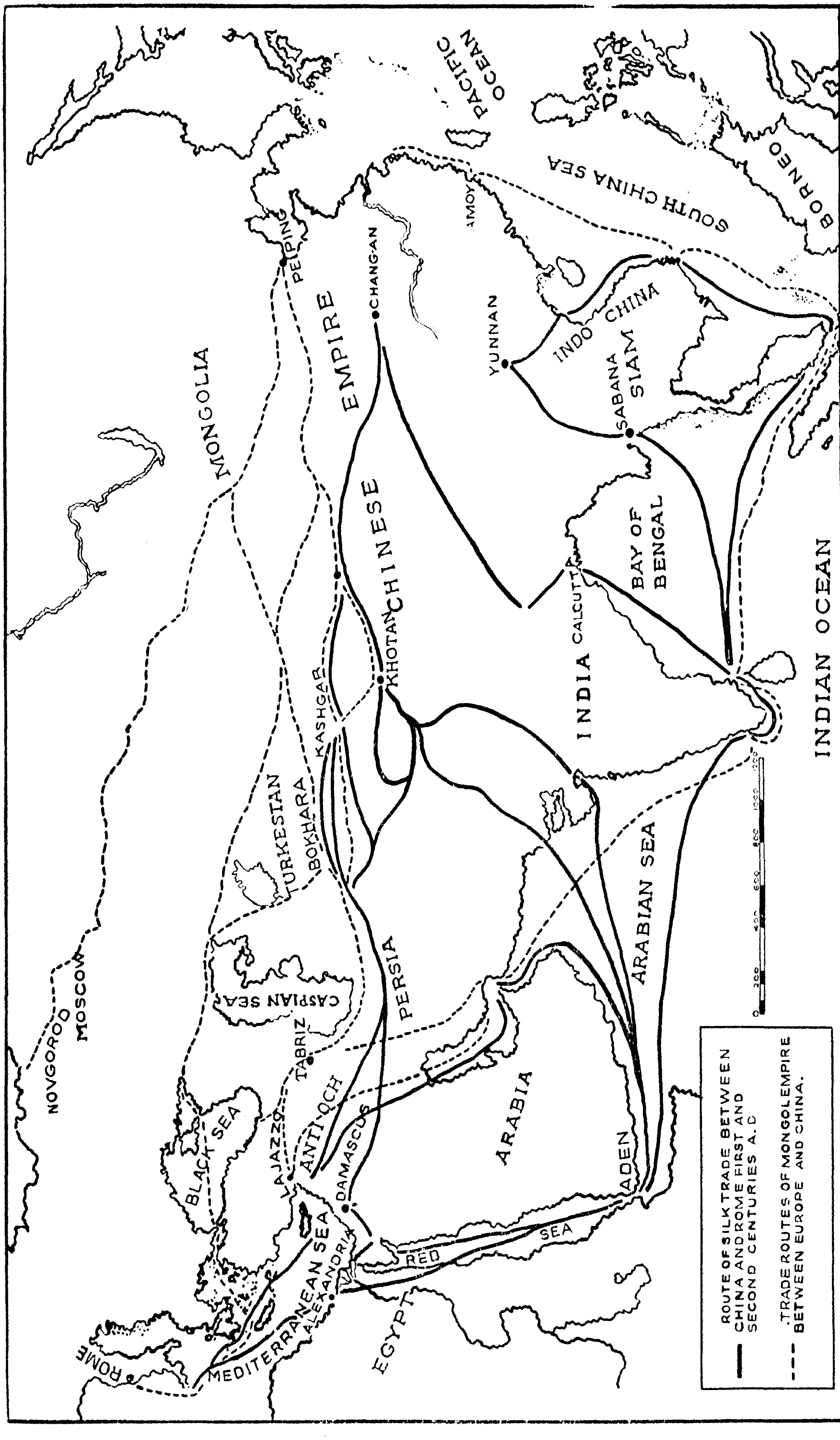


FIG. 7. — Trade routes between China, India, and Europe over which silk and spices and plants were carried. Drafted by C. C. TEBBUTT.

presumably fictitious name of APULEIUS PLATONICUS. He seems to have been neither Roman nor Greek but may possibly have been a native of north Africa.

This fourth century herbal was ostensibly an atlas of plants in which the descriptions were omitted, the idea being that the native plants could be identified by the pictures. The oldest copy extant is on parchment and is in the abbey of Monte Cassino in Italy. It contained about 130 representations of medical plants and was based on DIOSCORIDES and the *Medicina Plinii*. The original figures must date back to very early times and probably represent a school of phytography derived from late Roman art. This herbal of PSEUDO-APULEIUS merits attention because, being copied frequently, it had a very great influence during the Middle Ages. Undoubtedly it was the most practical and the most widely used book of remedies then in existence. The manuscripts were often interpolated with alien texts in the course of time, *e.g.* prayers, charms, and conjurations were added, also pictures of people who used some remedy or other, or had had it given to them.

In the fifth century the Roman Empire of the west fell, a victim of the insidious forces which had weakened it for so long.

This was the time of ST. AUGUSTINE, one of the greatest fathers of the Church. Although primarily a theologian, he developed the idea of potential creation which implied a theory of evolution.

A beautiful manuscript (BODLEY 130), the Herbal of APULEIUS BARBARUS, from the early 12th century, has been described by GUNTHER (1925). It contains descriptions of 130 plants in as many chapters according to a uniform system. This herbarium was based on the real DIOSCORIDES and on the *Medicina Plinii*, while the lists of synonyms, which are similar to those prefixed to the alphabetical Greek manuscripts of DIOSCORIDES, also include some plants of a North African origin. In several ways the work of APULEIUS shows the transition from heathen to Christian medicine. APULEIUS was a pagan, and in the oldest manuscripts the names of herbs are followed by prayers and incantations to be recited on gathering them, handed down, perhaps from ancient Greek or Tuscan herbalists. Early monkish transcribers Christianized the work by a slight alteration of the prayers; but in later medieval editions, these are either omitted, as in the Anglo Saxon version, or replaced by the Creed and Paternoster, which, declared the Canons of the Church, were alone to be repeated on such occasions.

The Herbarium associated with the name of LUCIUS APULEIUS MADAURENSIS, the famous philosopher and author, is now believed to have been a much later production, probably a Latin compilation of the fifth century.

COSMAS INDICOPLEUSTES, born in Egypt, probably in Alexandria, wrote a book on geography, 534 to 547, entitled "Christian Topography". This work is of great interest, though the author's aim was chiefly to refute the theory that the earth was round, and to prove that MOSES' tabernacle was a model of the universe. He was probably a Nestorian Christian. Indicopleustes means the India-traveller. He visited Ceylon, India, Ethiopia, and the Sinaitic Peninsula and knew the sources of the Blue Nile. He was at Adulis, Ethiopia, c. 525, and copied the Adulitic inscriptions referring to the expedition of one of the Ethiopian kings into Asia, 247 B.C.

While primarily a geographer, he wrote something about the plants which he saw in the Far East, about the pepper tree, for instance, which he said, winds itself around another stronger tree for support, like a grape vine. "Each fruit has a two-leafed green, like the green of the rue". He refers also to the sandal wood, and to a large nut called "Argellia", which may possibly have been the coconut.

This was the time at which the Codex Aniciae Juliana was written and when the first great monasteries were founded in which learning was conserved during the Middle Ages, although science was at a low ebb.

The age of JUSTINIAN (527-565) marked a halt in the general decline of Europe. The age is celebrated for the codification of the civil law of the empire and for the emancipation of Europe from the tyranny which Persia had maintained over the silk trade (fig. 8). Whether the imports from China came by land or water, it was always the Persians who first received them, and they watched jealously to see that it reached the Eastern Roman empire through no other hands than their own. Costly and prolonged war was waged on this account. By a combination of wars and devious diplomacy the control of Persia was broken, but it was finished by the introduction of silk culture into Europe.

Two Nestorian monks (ironically enough, they were Persians) who lived in China became familiar with silk worm culture and believed that it might be possible to duplicate it in southern Europe. The monks perceived that the transfer of living worms from China to Europe would be impossible, but the eggs could be carried to any country, however remote. They accordingly hollowed out their canes, filled them with the precious eggs and thus bore away, undetected, a richer spoil than had been won by battle or conquest. The mulberry tree grew best in Greece, but careful work under the direction of the monks was required to develop the silk industry. By the time of the Crusades, however, silk manufacturing had been developed, not only in Greece, but also in Italy and Sicily.

In spite of certain palliatives, the decline of the Empire was on its way. By the order of JUSTINIAN the schools of Athens were closed. In the years that followed, the barbarous nations from the north converted the Roman Empire into a desolation and then settled themselves in the ruins. In the seventh century the Latin language ceased to be spoken in Italy. In 732 the Saracens were defeated by CHARLES MARTEL at Tours. In 800 CHARLEMAGNE was crowned. As far as the plant sciences are concerned, centuries passed without any progress. It is true that herbals were copied, often with falsification, since no one had the wit to make any attempt at verification or investigation, but the Schoolmen smothered the spirit of science.

The *Macer Floridus de virtutibus herbarum* was written in the second half of the eleventh century. This is a poem describing in 2269 hexameters the virtues of 77 herbs and roots not based on original observations, yet it is very important, for it is one of the earliest Western documents proving a revival of interest in botany. Its immense popularity from the tenth century almost to our own time, is attested by numerous reproductions in manuscript and print. Its contents are based on the Medicina of PSEUDO-PLINIUS, on the Olera of GARGILIUS MARTIALIS, on an early

Latin translation of DIOSCORIDES, etc. The authorship of this treatise has been considerably discussed, and the question is not by any means settled, though it seems highly probable that it was written by ODO OF MEUNG on the Loire about the end of the eleventh century.

Chinese writings:- In China herbals and monographs of distinction were written in the 11th and 12th centuries. If one may judge from their contents, the quest for knowledge of plants received the attention of eminent scholars who were frequently rewarded with royal favors.

The Chêng Lei pên ts'ao (1108) written by T'ANG SHENWEI, a physician of SHU (now western Szechwan) during the Sung period, is a very important work, for in addition to being the best of that period it is also a repository containing much material from works the originals of which are long since lost. There were 31 *chuan* (books) which when completed he called "The Herbal of Chêng Lei" and sent to the Imperial Court. It was distinctly a medical herbal or "book of simples" and must have been very well known since it was republished many times.

Sorghum vulgare Pers. is one of the important cultivated grains in China, where it is known as "Kao liang", "Shu shu", etc. Recent studies by HAGERTY have shown that the plant was introduced during the Southern Sung period, 1127-1278. What appears to be the first authentic account of this grain occurs in a work on agriculture and sericulture published in 1273. Some Chinese writers attempt to place its culture in the pre-Christian era but their claims seem rather fantastic. Through an error in interpretation its introduction into China is attributed to the third century. The perpetuation of the error in subsequent Chinese works has been the cause of much confusion in writings concerning the distribution of this grain. Based upon linguistic evidences, it would seem that *Sorghum vulgare* Pers., originally came from Abyssinia and was introduced into China from India.

The early culture and utilization of *S. saccharatum* Pers. in China is well-documented in T'AO HUNG-CHING'S (452-536) book, quotations from which are given in the *Pên ts'ao kang mu* and other Chinese herbals. Owing to its classification as a fruit, accounts concerning it were separated from *Sorghum vulgare* Pers., which was placed in the grains classification. The Chinese ate the raw canes, cooked them to make a syrup and a crude sort of sugar.

Several outstanding works on cultivated trees also appeared in China in the 11th and 12th centuries.

TS'AI HSIANG wrote a treatise on the lychee in 1059 in which he records many important facts about the tree and shows great facility in botanical description. The name of the monograph was Li-chih-p'u. From data furnished by M. J. HAGERTY, we learn that TS'AI HSIANG (1011-67) was a noted scholar and trustworthy public official of the Sung dynasty.

It is a matter of abundant record that the lychee is an important product of China and that no less than nine special monographs have been written on it. The author gave a description of the area over which the lychee is grown, a critical discussion of the horticultural varieties, the climatic conditions suited to the

tree, its principal insect pests, the longevity of the tree, production and export of the fruit, methods of preserving the fruit, and other subjects. As a piece of botanical workmanship it is unsurpassed for the accuracy of its descriptions of the color and the form of leaves, the size and appearance of the fruit, accompanied as they were by illustrations. The appearance of this remarkable monograph a few years before the conquest of England by WILLIAM OF NORMANDY is an indication of the early development of horticulture in China.

A monograph on the oranges of Wên-Chou, Chekiang, written in 1178, is of even greater interest because of the accurate descriptions. Its author was HAN YEN-CHIH, eminent prefect of Wên-Chou. The work contains descriptions of 27 kinds of citrus fruits (sweet oranges, mandarine oranges, and kumquat) with discussion of the culture of the trees, adaptability of soils to citrus trees, control of harmful insects and fungi, and harvesting the fruits. Its special excellence is in the description of the fruits of each variety in which he gives the shape, texture of the rind, color, juice content, flavor, aroma, and keeping quality. The treatise compares favorably with those of modern times.

HAN YEN-CHIH, for example, wrote:

> The T'ien kan is similar in appearance to the Tung-t'ing Kan but its tree grows higher. Every fruit contains eight segments. The skin turns to yellow before the frost comes. The fruit is much sweeter than other Kan and it ripens much earlier . . .

He stated that both the Kan (mandarine) and Chü (sweet orange) are suited to "nitrous soil" and succeed better near the rivers or sea. Wherever planted, the soil must be well drained by ditches. River mud should be spread around the roots of the trees in winter, irrigation water and liquid manure ought to be given in the summer. "Those who succeed in making the leaves abundant and fruit plentiful will be regarded as the best gardeners". HAN YEN-CHIH was surprisingly modern in his directions for pruning the trees, for control of insect and fungus parasites, for harvesting and storing the fruits, and so on.

Islamic science:- The extraordinary rise and development of Islam contributed very little to the plant sciences, but it formed a haven in which many of the classical works were protected from the destruction and devastation suffered by true learning in Europe. The followers of the Prophet were practical, not scientific, people. For centuries untold they had wrested a living from an arid, inhospitable soil. The palm trees of the oases and the milk and flesh of their flocks were their principal sources of sustenance. The Arabic schools profoundly venerated ARISTOTLE and other Greek scholars, but they made no claim to originality.

The extraordinary beginning of Islam is so well known that, in spite of its tremendous importance, the briefest account of it will be sufficient. MOHAMMED was born at Mecca about 570, felt a call to prophesy in 610, and began to do so about three years later. The critical time of his life came in 622 when he migrated with his followers from his indifferent native place to Yathrib, later named al-Medina, *i.e.* the city of the Prophet. This time of crisis was called the Hegira, and fixes Moslem chronology. MOHAMMED died in 632. The Islamic world reached a position of power, splendor,

and prosperity about 750 as the result of capable rulers. The translation of Greek works was encouraged and we find today in various libraries beautifully illustrated manuscripts of DIOSCORIDES and commentaries on GALEN. Several important works of the latter have been preserved for us in the Arabic translations although the Greek originals were lost.

From the eighth to the twelfth century, pharmacy reached a high stage of culture among the Arabs owing to the careful study they gave to the valuable drugs produced in their country. Arabia was the habitat of the trees and shrubs that supplied the then known world with aromatic gums and valuable spices, such as olibanum, myrrh, cinnamon and cassia, and commanded the main trade route of the spice merchants from east to west, which also brought the Arabs in contact with the Orient. They also cultivated the study of chemistry which they brought to bear on their knowledge of plants and herbs. The Arabs produced no purely botanical works in which either the nature of plants or their relationships were discussed. Even ABUL ABBAS, called "The Botanist", and IBN BAITHAR, surnamed ALOSCHAB, — the two men who knew most about plants — wrote only as DIOSCORIDES, on the medicinal uses of plants.

The conquering tribes spread westward from the Persian Gulf along the northern coast of Africa, across the Mediterranean into Spain, carrying with them their *mores*.

The Arabs covered the countries which they settled with networks of canals, giving to Spain a system of irrigation by pumps, water-wheels and floodgates. They established the culture of silk, the manufacture of paper and other textile fabrics in Spain. Whole tracts of land which now lie barren were once covered with olive groves, and the environs of Seville alone, under Moslem rule contained several thousand oil factories, according to AMEER ALI. Some of their plant introductions such as alfalfa and almond still bear their Arabic names. The Arabs brought also their fine orchard and garden fruits, many of which were originally from Persia, together with others like ginger, saffron, and myrrh. When the Spanish and Portuguese went out to colonize the New World in the 16th century they brought with them these Arabic crops and domesticated them in the Americas.

ABD-ER-RAHMAN I (757-788) formed Spain into an independent caliphate, and in the eighth century, Cordova became the center for the teaching of science and was made the Moorish capital. This caliph laid out a botanical garden at Cordova, caused rare plants to be collected in Syria and other parts of Asia, and planted the first date palms to be grown in Spain. The libraries attached to the mosques were centers of activity for scribes, notaries, and secretaries who sat at the feet of a master. Cordova was a center of learning four centuries before Paris or Oxford; a civilized city with lights and water and general culture six centuries before Paris or London; Moorish Spain had at one time seventy public libraries; Cordova's library had 600,000 volumes. In the ninth century an Academy of Science was founded at Bagdad.

Arabic writers began in the eighth century to produce a special type of literature on natural history. ALL-ASMA'I OF BASRA (740-828) composed books with the following titles: "On the horse", "On the camel", "On plants and trees", "On the vine and the palm

tree", "On the making of man". IBN WAHSHIYYA (ca. 800) composed the Nabathean agriculture, a book which contains some useful information on animals and on plants and their cultivation mingled, however, with legends and forged translations from Babylonian and other Semitic sources. The book of Spanish agriculture by ABU SECHARJAH IBN ALWAM was written in the 12th century.

The medical writers of Islam are justly renowned and exerted a strong influence on the practice of medicine in Christian countries.

A Persian herbal of the tenth century A.D. was written by ABU MANSUR MUWAFFAK BIN ALI HARAWI (see SARTON, History of Science I, p. 678). It was concerned chiefly with medicinal plants and is strongly reminiscent of DIOSCORIDES. One finds in it many words of Sanscrit origin, so it would seem that the author included plants introduced from India.

Concerning this work the author said:

I have searched in all the books of the wise men and the doctors who have written much, and have industriously studied their writings on the simple and the compounded medicaments and foods, in addition I have studied the effects of the remedies, their uses, their bad effects, and their characters which fall into four grades.

Of the 584 substances discussed in relation to pharmacology, practically all are of vegetable origin. The following passages show the nature of the herbal:

Idschas, the plum. There are several varieties of the plum. The best are the garden plums; these make the body supple. They drive out the yellow bile, especially when it is sour. They ease the discomfort of the heart, which is caused by heat. They diminish the yellow bile and retard sexual desires . . . If one washes the mouth or gargles wine in which leaves have been boiled, he alleviates all complaints of catarrh which exist in the throat, neck, and chest. The gum of the tree eradicates herpes and blemishes of the skin . . .

Utrudisch, *Citrus Medica,* the citron. It is of four constituents. 1. The rind is like fire, hot and dry in the second degree. It sweetens the breath and strengthens the stomach. Its effect resembles that of cinnamon. 2. The flesh is like water, cold and moist in the middle of the first degree. It is hard to digest, therefore bad for the stomach; it causes gas and colic pains. The concentrated sap is stronger and hotter in consequence of the honey and the hot medical principles which are mixed therewith. 3. Its sap, the so-called acid is, like the earth, cold and dry, at the end of the second degree, it diminishes the yellow bile, relieves the palpitation of the heart caused by the heat, and supports the body. The acid removes warts and black spots and dispels the ictheric yellow color of the eyes when you drop it into the eyes. 4. The seeds of the citron are like air, hot and moist in the middle second degree. They are hard to digest, used against haemorrhoides, and work efficiently as an antidote for scorpion bites if one puts two Miskals (12 g.) into the food and takes it, or applies finely ground seeds to the place where bitten. The leaves are similar in effect to the rind, but in temperament, resemble *Melissa officinalis.* Chewing the leaves make the breath fragrant and removes the odor of onions and garlic from the mouth. GALEN says that the oil of the citron rind may be of use in paralysis of the face and in paresis of the extremities; also it may be used for scorpion bites as well as the oil of the seeds. The Chinese orange also acts as a strong antidote when dried, pounded fine and mixed with honey. Its concentrated juice discharges the yellow bile and suppresses nausea; it increases sexual desire and is in general similar to citron juice.

Tamr, *Phoenix dactylifera.* The dates are difficult to digest but very nourishing. Consequently they strengthen the body, increase the blood and the semen. Almonds and the poppy alleviate the harmfulness of the date, even so the Sikangabin if one drinks it afterwards . . . The best dates are those from "Hirun", after them come the yellow; the darker they are, the worse. After eating them one should eat pomegranates or drink Sikangabin and sugar, or vinegar and rose water to which *Rhus coriaria* was added.

Tamr ul-hindi, *Tamarindus indica.* The Indian tamarind is, like the plum, moist, but reduces and weakens. It is cold and dry in the second degree. It consists of fiber, seed, and jelly. It represses the heat and the yellow bile, stops nausea, softens the body, and allays thirst. It dispels the yellow-bile fever, but is harmful to lungs and chest.

Thum, *Allium sativum,* garlic. The garlic is a means whereby the health is perpetuated because it has the power to prevent stagnation of the blood. It is at the same time a food and a useful remedy. The garlic which grows wild . . . is employed against corrupted humors. The garlic is advantageous to the body so long as it is sound, but not to the poisoned body; on that account it acts as an antidote for deadly poisons, and snakes flee away from it. We should not be without it in any kitchen, nor leave it out of any food, nor despise it on account of its unpleasant odor . . . it drives away the toothache if you bruise it and lay it upon the tooth . . . it cures baldness by stimulating the growth of hair . . . it increases the natural heat of the body, and promotes digestion.

Rumman, *Punica granatum,* the pomegranate. All kinds of pomegranates act as astringents and make the teeth short. The sweet pomegranates counteract heaviness of the stomach resulting from acute catarrh if they are taken with roasted barley meal.

It is evident that the writer was giving, as completely as he was able, the pharmacological knowledge of his day for the benefit of all who could read. He seems to take for granted a knowledge of plants on the part of his readers, for he does not give any characters of a plant which would enable one to identify it. Although he often quotes GALEN, he seldom mentions DIOSCORIDES. Yet there is much to suggest that he borrowed extensively from the latter.

IBN SINA (980-1037), known to the world as AVICENNA, was a man of unusual talents. He was a Persian by birth and a lifelong student of botany. The Canon of Medicine which he compiled is an encyclopedic work, which, after being translated into Latin in the 12th century by GERARD OF CREMONA, had a great vogue in Europe. In the last 30 years of the fifteenth century, it was issued 16 times, 15 editions being in Latin, one in Hebrew. In the following century there were more than 20 editions.

AVERROES (1126-1198) a native of Cordova was the greatest nature philosopher of the Middle Ages. In his philosophy he followed ARISTOTLE and his principal work took the form of commentaries on ARISTOTLE.

AHMAD AL-GHAFIGI was born in Andalusia near Cordova and, although the dates are uncertain, we can place him in the 12th century. His "Book of Simple Drugs" consisted of abridgements from the writings of DIOSCORIDES and GALEN, adding the recipes of later physicians just as ABU MANSUR MAWAFFAK had done earlier.

IBN BAITHAR, born at Malaga, travelled in search of plants in Tunis, Egypt, Greece, Syria and as far as Medina and Mosul. He died in 1248 at Damascus. He was probably a better botanist than

any other Arab named, for he described about 1400 plants, and described only what he saw. In addition to the various works on medicinal plants he wrote a book on lemons which was translated into Latin by ANDRES ALPAGO and published in Venice in 1583 and in Paris in 1602.

While the system of feudalism was establishing a centralized aristocracy in Frankish Gaul, the Saracens had obtained control of the Mediterranean. By the middle of the ninth century Islam was a formidable Mediterranean power and deprived Christian commerce of its opportunity for travel and trade until the eleventh century.

When Arabic science came to a standstill about 1100, botany had lost all pretense to originality and had become merely a list of drug plants.

We owe a debt to the Islamic world for harboring the classical results and writings of the Europeans, adding to them some of the plant lore of the Orient. The indifference of the medieval European to Islamic science was stupendous, as shown by the paucity of knowledge of the East brought back by the Crusaders. There were, however, a few narrow channels in Italy and Spain through which some of the learning returned.

Salerno on the Bay of Paestum, Naples, was the seat of a school which preserved some traces of Greek medicine. Paestum was originally a Greek colony. A medical corporation existed at Salerno as early as the ninth century. We may be sure that those early Salernitan physicians had some acquaintance with Greek medicine. The traditions of Greek medicine had never been entirely interrupted in South Italy and in Sicily; definite traces of it being found as late as the seventh and eighth centuries. Barbarian, Latin, Greek, Jewish, and Moslem influences were naturally and gradually synthesized and produced the first medical school of Europe at Salerno. The influence of that school grew rapidly during the second half of the 11th century and even more so during the 12th. The first Crusade (1096 to 1099) gave it a considerable impetus. (See also fig. 28).

A Tunisian adventurer with a shady reputation, CONSTANTINE THE AFRICAN, passed several years at Salerno before he took holy orders at the famous monastery of Monte Cassino in Campania, where he took up the work of translation about 1070 and translated many works from Arabic into Latin. His influence on the School of Salerno was transitory, although his translations from the Arabic writers played a unique part in introducing Islamic culture into Europe. CONSTANTINE's Latin versions are often inaccurate and confused, but they are typical of much of the Barbero-Latin literature of the Middle Ages. He was often dishonest, claiming for himself many works which he had translated from Arabic. Nevertheless, CONSTANTINE did bring back some of the culture of the Greeks which had been salvaged by the Arabs and Persians.

In 1085, the Spanish Christians defeated the Moors at Toledo and captured the city which had been the greatest center of Moslem learning in the West. Latin scholars then began to go to Toledo. The best they could do was to translate. The intermediaries for the learning, and later on for the translations, were native Jews and former Moslem subjects (Mozarabs). The library in Toledo was a fountain of knowledge to which prominent men came from

many places in Western Europe. Archbishop RAYMOND founded a school of translation which continued to the thirteenth century, utilizing the services of polyglot Jews who spoke Arabic, Hebrew, Spanish, and perhaps Latin. GERARD OF CREMONA (born 1114) went to Toledo where he worked for twenty years translating important Greek and Arabic works with the help of Jews and Christians.

Palermo, Sicily, was another center of scholarly scientific work under Emperor FREDERICK II who was really interested in biology. His collection of living animals was remarkable. Under FREDERICK's patronage, MICHAEL SCOT translated the biological and zoological works of ARISTOTLE from Arabic and Hebrew versions.

REFERENCES:

GARGILIUS, M. Quintus (1828, 1831): . . . De arboribus pomiferis. (*In* MAI, A. Cardinal, ed.: Classicorum auctorum e Vaticanis codibus editorum. tom. 1:391-413; tom. 3:418-426).

GROFF, G. W. (1921): The lychee and lungan. Orange Judd Co.

HAN YEN-CHIH (1923): HAN YEN-CHIH's Chü Lu (Monograph on the oranges of Wên-Chou, Chekiang), trans. by M. J. HAGERTY (Extrait de T'oung Pao, 2. sér., vol. 22).

HAWKS, E. (1928): Pioneers of plant study. The Sheldon press, London; Macmillan, New York and Toronto.

HEARD, G. (1937): The source of civilization. Harper, New York.

HUDSON, G. F. (1931): Europe and China. Arnold, London.

MARCELLUS EMPIRICUS (1916): Marcelli De medicamentis liber, recensuit Maximilianos Niedermann. (*In* Corpus medicorum latinorum, v. 5).

MEYER, E. H. F. (1854-57): Geschichte der Botanik. Gebrüder Bornträger, Königsberg.

REYES PRÓSPER, E., ed. (1917): Dos noticias históricas del immortal botánico y sacerdote hispano-valentino Don Antonio José Cavanilles . . . Artes gráficas Mateu, Madrid. (Contains a bibliography of Islamic writings on plants).

Chapter V.

THE RENASCENT PERIOD.

The intellect of Europe did not suddenly waken after the long sleep of the Middle Ages, but about the 13th century there were some confused strivings at places and some awakening of minds at others. The uncritical attitude and slavish devotion to dogma were destined to disappear, not suddenly, but after a long struggle against medieval conceptions of God, man, and the world. What men have learned about the cosmos in which they live has been won at tremendous cost.

An interest in natural philosophy first showed itself in the revival of encyclopedias. A few men conceived the plan of putting into writing their ideas on the world in which we live, and, while these were obviously incomplete, they eventually awakened an interest in observation and experiment.

Encyclopedic writers:- We may start our survey with ALBERTUS MAGNUS, "Doctor Universalis" (circa 1193-1280). His name was originally ALBERT VON BOLLSTÄDT and he is known to have belonged to a noble Suabian family. Concerning his early years little is known with certainty. He entered the university of Padua where he found a congenial environment and where he probably first familiarized himself with the philosophy of ARISTOTLE. Here he quickly won the admiration of students and teachers, and here he entered the order of Dominicans. There can be little doubt that ALBERT possessed one of the greatest minds of all time and that he merited the title frequently applied to him of the "Aristotle of the Middle Ages".

His life was enriched with various experiences and full of achievement. In addition to his ecclesiastical interests, he had an extensive knowledge of geography, astronomy, medicine, botany, and zoology. After teaching at various places in Germany, he was sent to Paris, where, from 1245 to 1248, he expounded the doctrines of ARISTOTLE. One of his pupils was THOMAS AQUINAS. In 1259 Pope ALEXANDER IV appointed him bishop of Ratisbon, but he retired to a convent in Cologne in 1262 to devote himself to the adaptation of Aristotelian philosophy to the use of the Latin races. His success in this great task is noteworthy because of the prevailing opposition to ARISTOTLE's doctrines on natural science and metaphysics which had been created by the condemnation of the school of Paris in 1210, 1215, 1231, and 1245.

He had the courage to reject some superstitious ideas but continued to believe in many others, and his writings are not deficient in medieval traits and symbolical imagery. This simply illustrates how difficult it is to emancipate the mind from accepted ideas in a lifetime. He not only reconciled his theories with Christian orthodoxy, but eagerly included fresh information, whatever its

source. He realized that scientific information cannot be attained without investigation, and even recognized to a small extent the value of experimentation, but he was, nevertheless, often uncritical and awed by authorities. His writings on all subjects fill 21 folio volumes. MEYER gives an extended synopsis of his botanical writings.

In attempting to estimate the value of the scientific work of ALBERT we must keep in mind the mental attitude of the people and the methods of promulgating knowledge in his day. With all his medieval backgrounds, he did exhibit genuinely scientific traits. The excellence of his work is the more amazing when we realize that he had neither microscope nor chemical reagents.

De vegetabilibus, the botanical work, is based on that of NICHOLAS OF DAMASCUS which ALBERT believed to be ARISTOTLE's. De vegetabilibus was widely distributed and widely read in the thirteenth and fourteenth centuries, not only in the cloisters, but also in the farm houses and homes. PIETRO DE CRESCENTIIS made liberal use of ALBERT's work. He drew heavily on the writings of AVICENNA (IBN SINA) for his information about the medicinal uses of plants. Eventually ALBERT's botanical work was almost forgotten until MEYER of Königsberg rediscovered the famous work and emphasized its tremendous importance.

De vegetabilibus is a medical herbal only incidentally; it is, primarily a book of plant descriptions with a discussion of certain philosophical questions. He dealt, moreover, with plants he knew, and not with fabulous fictions about them.

ALBERT's ideas on plant morphology are the first on record since the time of THEOPHRASTUS, but as he did not know THEOPHRASTUS' writings he must be credited with originality. He observed that thorns are stem structures, while prickles are superficial; that a cluster of grapes is sometimes replaced by a tendril, *ergo,* the tendril must be an incompletely developed flower cluster. He recognized the pentamerous symmetry of the wild rose and of the apple core. His description of the fruit of the apple with its three coats; the five-chambered core, the floral receptacle above, the seeds with the testa, and the two hemispherical cotyledons, is a masterpiece.

ALBERT believed that species are mutable but we find in his writings no theories of the evolution of organic life. He grappled with the problem of plant classification on which no progress had been made since THEOPHRASTUS roughly divided plants into trees, shrubs, and herbs. According to STRUNZ, ALBERT's classification was as follows:

- I. Leafless Plants (mostly cryptogams)
- II. Leafy Plants
    - 1. Plants with cortex or bark (Monocotyledons).
    - 2. Plants with tunica (Dicotyledons).
        - a. Herbaceous, without nodes.
        - b. Woody (ligneous), with nodes.

The logic of this classification is certainly appealing to a modern botanist.

Since ALBERT wrote about plants for the people of his time, he described things that he saw. The rule of the Dominican Order required its members to travel on foot, consequently, he had abun-

dant opportunity to observe the flora of Germany as he travelled back and forth across the land on ecclesiastical missions. His freedom from sophistry was due, to some extent, to the fact that his feet came into contact with the soil where plants grew.

According to ALBERT, wheat prefers heavy soils; the first growth is mowed or pastured off, that it may not run too much to straw, for rank straw has little grain. Wheat grain produces the best and most desirable bread. Without bran the flour gives the most nourishing bread, with bran it is more digestible. The beech (*Fagus sylvatica*) makes the best fuel, or charcoal, but is poor building material because it is very susceptible to injury by insects. The young leaves serve as food for man and the nuts are used for cattle feed although they do not produce as solid flesh as that obtained by feeding with acorns. The oak (*Quercus robur*) and its acorns are carefully described. The wood is almost as good as birch for wood carving. The gall-apples "in which a little worm grows" were used at that time for the manufacture of black ink.

Cultivated plants of the orchard and garden were of great interest to ALBERT; he was naturally familiar with vineyards and grapes, having passed many years in the Rhine valley. The Walnut tree (*Juglans regia*) is planted in deep holes and at distances wide enough to permit them to reach their normal size. He advises that one should frequently scoop out basins around the trees, so that the fruits should not be blank, and that one should split the bark of the trunks from above downward, so that the "modern part" may harden. This practice, according to ALBERT, should be followed for almost all trees. The walnut tree does not bear flowers, only long green outgrowths (purgamenta). He pointed out that the tree is unfavorable to surrounding cultivated plants on account of its "indwelling extreme toxic bitterness" — a fact recently "discovered".

The vegetable garden, according to ALBERT, should be on a soil which is rich and well watered. On that account it should have a spring or a pond, or at least a cistern, in which to store rain water. The garden work as a rule should begin in March, but for early and abundant vegetables it should be started in September. After being sown, the seedlings stand too close together and therefore should be transplanted, so that each may have sufficient room for development. Great care should be taken to protect the garden plants against damage by animals. Soot is to be strewn against worms; fresh seeds soaked in wine are to be used against caterpillars, while ants are repelled by the heart of a night owl laid on their hills.

ALBERT named and discussed turnips, radishes, carrots, cabbage, lettuce, endive, spinach (mentioned for the first time in Europe), chenopodium, mustard, cress, cucumbers, and savory plants for seasoning, summer savory, lemon balm (*Melissa officinalis*), thyme, fennel, onion, saffron, and medicinal plants, such as parsley, celery, elecampane, salvia, fenugreek, etc.

BARTHOLOMAEUS ANGLICUS, another encyclopedic writer of the 13th century, was an English Franciscan of whose life little is known. He lived until about the middle of the 13th century. He studied at Oxford, joined the religious order in France, and was a lector at Paris about 1220 and at Magdeburg about 1230. His

broad knowledge of theological, philosophical, and scientific subjects had a great influence on the world in which he lived and moved. The work entitled "De proprietatibus rerum" (c. 1230-1240) was widely circulated for upwards of three centuries and was translated into several European languages. Students in the universities, as well as the laity, read it eagerly. It is said that it was one of the books which the students in Paris could hire for their perusal. The book is important for the historian of science because of BARTHOLOMAEUS' discussions of geography, psychology, anatomy, physiology, disease, plant and animal life, etc.

THOMAS OF CANTIMPRÉ, also known as THOMAS OF BRABANT, was a Dominican who lived in Cantimpré near Cambrai in what is now Belgium in the thirteenth century, and died, probably in Louvain, c. 1271-1280. He may have attended some of ALBERT's lectures, but can hardly be called the latter's disciple. His two main works are (1) "De natura rerum", a popular encyclopedia of science, to the preparation of which he devoted some fifteen years of study and completed it between 1228 and 1244; (2) "Bonum universale de apibus", a collection of droll stories for the edification of the clergy.

THOMAS' De natura rerum was translated into the vernacular German by KONRAD OF MEGENBERG and published under the title of Puch (Buch) der Natur.

We may step ahead temporarily to speak of this Puch der Natur, published about two hundred years after the time of THOMAS OF CANTIMPRÉ. The first edition seems to have appeared in 1475. It was almost entirely a translation of De natura rerum, although some have thought that the material was drawn from De vegetabilibus of ALBERTUS. The following excerpts will show the type of plants mentioned.

IV. A. VON DEN PAUMEN

Wir schüllen nu in disem vierden stuck des Puoches sagen von allerlai Paumen und des êrsten von gemainen paumen, dar nâch von wolsmeckenden und gar edeln paumen . . .

Erln = *Alnus*
Mandelpaum = *Amygdalus*
Puochen = *Fagus*

V. VON DEN KRÄUTERN

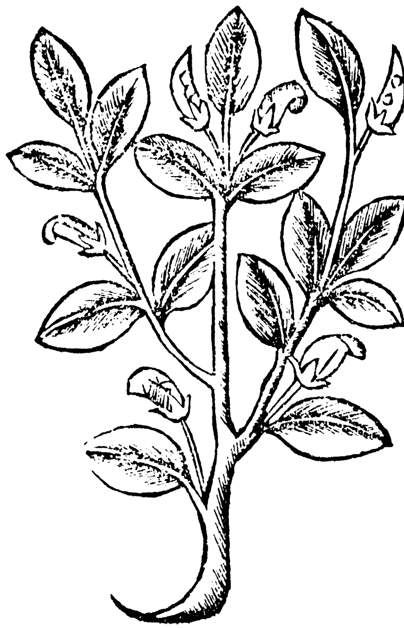
An disem fünften stuck des puoches shüll wir sagen von den kräutern, und des êrsten in ainer gemain.

Wermuot = *Absinthium*	Patonigen = *Betonica*
Anetkraut = *Anethus* (Dill)	Basiligen = Basil = *Ocimum*
Epf = *Apium*	Saffran = *Crocus sativus* (Saffron Crocus)
Knoblauch = *Allium*	Alraun = *Mandragora*

Although there were no great advances in botany immediately after the death of ALBERTUS MAGNUS, there was a gradual awakening of the scientific spirit in Europe. Astronomy and physics were finding new ideas about the cosmos and substituting research for dogmas, in spite of unrelenting opposition on the part of the church. The discovery of the Americas demanded a revision of many respectable and staid ideas. There was a growing suspicion that after all the new ideas of the scientists might be right.

Invention of printing:- The European invention of printing from movable type about 1440 greatly aided the promulgation of ideas

on all sorts of subjects. Books then became the property of the laity as well as of the monks in the cloisters. Printing from type



Capitulũ.clxxxij.

Aba inuerſa. Pli. Faba inuerſa eſt
f herba cuius folia ſunt ſicut folia alke
kengi: ſtipes eius longitudinis cubiti
vnius aut duorum aut plus: ſemen eius viri-
de: tendens ad nigredinem: magnitudinis fa
be cõmunis: habens quaſi effigiem in medio
ſicut faſeolus: ⁊ romani vocãt eaꝫ fabariam.

Operationes.

¶ Fabaria ſiue faba inuerſa in vino decocta
ad teſtium tumores ac genitalium proficit.
¶ Fomento ẽt ex aceto decocto tũores matu
rat ⁊ aperit, Itẽ liuorib⁹ quoqꝫ cõbuſtis me-
det. ¶ Et ſvoci eã ꝓdeſſe Marc⁹ varro fatet
¶ Fabaruꝫ deniqꝫ ſiliquarũqꝫ cinis ad coxẽ
dices ⁊ ad neruorum veteres dolores prodeſt
cum vetuſtate ſuilli adipis: per ſe quoqꝫ deco
cte ad tertias cortices fabaruꝫ ſiſtunt aluum.

FIG. 8. — *Faba*. Probably *Vicia faba*. Ortus Sanitatis, Venetijs 1511 (Latin reprint of the original German Edition, Mainz 1485).

also eliminated the errors and the interpolation of the ideas of the copyists. The art of printing also came at a time when men were becoming inquisitive about the plant world. They had ranged

through field and forest for plants to make the brews and teas for their homely remedies. They had names for most of the local plants, but they yearned for more extensive knowledge. Hence it came that the first books were descriptions of plants and they were written by men who had had medical educations.

Classical herbals:- The name "herbal" was not coined for some time, but it is now in common use to designate one of those old books about plants.

It is now in order to mention and discuss briefly some of the historically important herbals.

KONRAD OF MEGENBERG translated and published Puch der Natur, as previously mentioned, in 1475. This work contains much that appears to us today as pure nonsense. Certainly the inclusion of fabulous stories about mythical creatures retarded rather than advanced the natural sciences. The botanical portion of the work lists the Latin and vernacular names of less than a hundred plants and gives their medicinal properties. It also contains the earliest known wood-block illustrations of plants published in Europe. The work must have found ready sale, if we may judge from the number of editions subsequently issued.

The Herbarium of APULEIUS (mentioned in the preceding chapter) was published in Rome in 1481 or 1483 by LIGNAMINE. The success of this herbal was also great, if we may judge from the scarcity of extant copies, even though it reproduced chiefly the superstitions and fabled plants of the Dark Ages. LIGNAMINE was not a printer, but he was a master at furnishing copy. Being enthusiastic about the possibilities of spreading knowledge by means of the printed book, he invited two German printers who had come to Italy, to set up their press in his palace. In addition to theological works, LIGNAMINE wanted to publish something new. He, therefore, gave the printers the manuscript of APULEIUS, which he had found in the Benedictine monastery of Monte Cassino. LIGNAMINE's name appears on the title page as the printer, but it is more probable that he was only the patron of the printers.

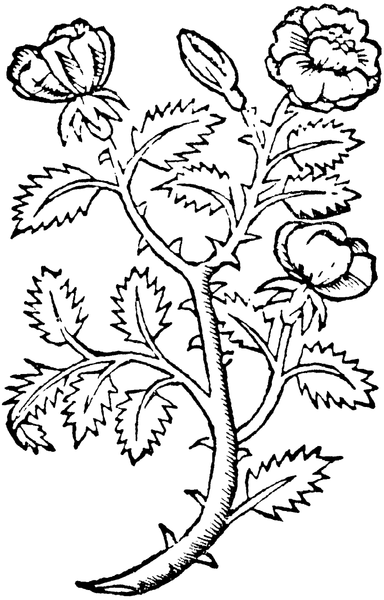
The Herbarius Latinus, the first herbal printed in Germany, although anonymous, was a compilation from medieval and classical writers. It was intended for the poor people and therefore described cheap and homely remedies such as could be found in field and forest. The text is in Latin, but all names of plants are given in German, as well as in Latin. It was published by PETER SCHOEFFER at Mainz 1484.

Gart der Gesundheit, a new creation in the vernacular of Germany with nearly 400 illustrations, was also published by PETER SCHOEFFER in 1485. This was not the work of a single author but a compilation worked out by the printer and the scholar like other medieval books. It was partly based on the Herbarius Latinus published the preceding year, but the text figures were printed from entirely new and more accurate cuts.

Many herbals were produced in the next twenty years in the Netherlands, France, Italy, Switzerland, and Germany. All were compilations and often translations of other herbals; sometimes a printer sold the wood-cuts to another printer.

The Ortus (or Hortus) Sanitatis was an illustrated Latin translation of an earlier Herbarius. Like all of the early herbals,

Capitulum. cccxcviii.



r Rosa latine. grece rhodon. ara. bard.
Serap. in lib. aggre. cap. bard. auct.
Galienu. viij. simplicium pharma. ca.
de rosa. Substātia eius est cōposita ex substan
tia aquosa calida cum duabus alijs qualitati
bus permixta stiptica scʒ ⁊ amara: cuius stipti
citas est in quantitate tali: quia corpora habē
tia virtutē fluxuū nō possunt dissoluere virtu
tem eius. ⁊ semen eius est magis stipticum q̄
rosa. Et ideʒ rosa cum stipticitate que est in ea
inest ei dulcedo ⁊ similitudo acuitatis vel inor
dinationis pauce. ⁊ cōuenit apostematibus ca
lidis in pncipio corꝝ: ⁊ oportet ꝙ recipiatur re
cens ex ea: ⁊ abscindantur sūmitates eius val
de cū forpicibus: ⁊ reseruentur pro medicamini
bus oculorꝝ. Sed oleuʒ rosarꝝ est in natura sua
medium iter naturā rose ⁊ olei. ⁊ ē medicina cū
qua curantur apostemata sanguinis i augmēto
ipsorū.

ipsorum: ⁊ in eo est virtus penetrādi ad pfun
dum corporis: ⁊ humectat corpa sicca: ⁊ cōquas
satur cū aceto ⁊ inungit caput cū eo: ⁊ cōuenit
dolori capitis facto ex caliditate solis: ⁊ qn̄ ro
se siccantur opʒ ꝙ desiccentur in vmbra: ⁊ cōmo
ueantur assidue: ⁊ aqua rosarū est frigidior cōple
xione tēperata. non tn̄ multuʒ: ⁊ ipsa qdem est
subtilis multe subtilitatis. ⁊ signum in hoc est
ꝙ rosa desiccatur cito. Ideo quia in ea non est
aliqua viscositas: qr odor eius vincit: ⁊ propte
rea festinat ⁊ replet vias odoratus.

FIG. 9. — *Rosa.* Ortus Sanitatis, Venetijs 1511 (Latin reprint of the original German Edition, Mainz 1485).

it is highly prized by bibliophiles, especially for its weird pictures of imaginary creatures. (A few of the best of these pictures have been reproduced in ARBER's "Herbals"). The buying public was no doubt interested in this book for many reasons, but chiefly because they sought remedies, cures, and palliatives in the animal and vegetable realms for their bodily and mental afflictions. The circulation of the book came to an end by the middle of the 16th century.

The writing and publication of new and better herbals was perhaps the chief botanical accomplishment of the 16th century. They served a great purpose in their day, but we cannot at present see evidence of such genius in them as that which characterized the next century. We must remember that the object in the minds of these writers was utilitarian. They were concerned with the medicinal properties of plants, much as DIOSCORIDES had been, and were anxious to depict the characteristics which should enable men to get the right plant for a particular purpose. The elegance of their work and the power of independent observation entitle the herbalists to our respect, although we must admit that they contributed little to the advancement of plant science, except by their success in accumulating knowledge of plants for a foundation for following generations.

Herbalists in Europe:- OTTO BRUNFELSIUS (BRUNFELS) was first in time among the German botanical reformers of the 16th century and first in rank. This industrious but pathetic man was born in 1464 at Mainz and died in 1534 at Berne. His earthly lot was certainly not a happy one. In early life he expressed the desire to enter the Church and to take orders. His father opposed the plan but OTTO, after he attained legal age, entered a Carthusian monastery in Mainz. Eventually he espoused the doctrines of LUTHER and renounced the religious order into which he had entered at the cost of family strife.

In Strasbourg whither BRUNFELS went, he participated in the Lutheran movement by preaching and writing. Unfortunately, he contracted tuberculosis which so impaired his voice that he could no longer preach. He therefore opened a school for boys when he was past fifty years of age. Moving to Switzerland, he obtained the position of city-physician in Berne shortly before his death. Our admiration for his excellent botanical work is enhanced by the thought of the vicissitudes of his life.

Herbarum vivae eicones was the title of BRUNFELS' botanical work published at Strasbourg in three volumes in the year 1530. BRUNFELS was chiefly interested in the medicinal uses of plants and intended to guide those who went to the fields to collect plants. The great merit of the work lies in the selection of material and the excellent phytography. The figures are a tremendous improvement on the crude wood-cuts of the 15th century herbals. His brief descriptions are in large part quoted from the writings of classical and medieval times. Each began with a list of the names in different languages followed by statements taken from ancient writers and concluded by his own idea of the plant and its qualities.

More than any other BRUNFELS' herbal may be considered as a link between ancient and modern botany. It is both the end of a long line of classical and medieval works on medicinal plants and the beginning of modern taxonomy. The text was virtually a com-

pilation of the writings of his predecessors, and in this respect is somewhat medieval in character. The illustrations on the contrary contribute something new, because they are life-like figures and not copies of previous pictures. They are so good that it is possible to identify most of the species represented. Unfortunately some of the figures do not correspond with the text. The mistakes may have been made by the printer. Among the species illustrated there are 47 which appear to have been new.

A few names from BRUNFELS and the modern equivalents may be mentioned:

25. *Herba paralysis, Flores clavium, Clavis S. Petri,* Geel Himmelschlüssel, Weissz Betonien I. 96. = *Primula veris* L.
46. *Viola sylvestris,* Wilde Violaten I. 137 = *V. hirta* L.
49. *Crus galli,* Kleiner Hanfuosz, I. 145 = *Ranunculus bulbosus* L.
68. *Hepatica,* Edel Leberkraut, Hyrszklee, I. 190. = *Anemone hepatica* L.
69. *Iecoraria,* Leberkraut I. 191. = *Marchantia polymorpha,* L.
128. *Acetosa, Lapathum acetosum,* Saurampffer, II. 72 = *Rumex acetosa,* L.

It cannot be truthfully said that BRUNFELS had any valid ideas on classification of plants. When he used the word "species" he did so in the general sense of "kind".

He mentions various plants which were grown in gardens for decorative plants or for their desirable odors. Yellow Bachelor's Buttons were used for bridal wreaths, and Monkshood was a favorite flower among the German matrons. The Stock and the Pinks were associated because of their clove-like odor. *Iris germanica* was grown as an ornamental plant as well as for the sake of its fragrant rhizome, which is one of the sources of orris-root.

The name of HIERONYMUS TRAGUS (HIERONYMUS BOCK) is associated in several ways with BRUNFELS, who once walked from Strasbourg to Hornbach (a distance of sixty miles) to urge BOCK to publish a new herbal in the vernacular. TRAGUS (or BOCK) had furnished various bits of material to BRUNFELS which the latter was pleased to use in his Eicones. BOCK wrote and published New Kreutterbuch in 1539, describing but not illustrating plants he had found in the woods and fields. However, the editions of 1546 and later were well illustrated. His descriptions of flowers are important indications that he comprehended things by which his predecessors had been completely baffled. He recognized the corolla, stamens, and pistils as essential parts of many flowers and apprehended something of natural relationships. He represented in one of the figures the root nodules of a bean plant, though he made no comment about them.

VALERIUS CORDUS (1515-1544) was the first to draw up botanical descriptions in a systematic form, studying the living plant in flower and in fruit, and including details about the types of plants, forms of the parts, colors, odors, and tastes. He began to note the anatomy of the various parts, for example, the number of chambers in the ovary, placentation, etc. and was the first to speak of pollen and to make a distinction between an umbel and a corymb. VALERIUS CORDUS died tragically in his 29th year after having written five books of his Historia Plantarum. CONRAD GESNER published the work in 1561-63, but saw fit to add 280 figures taken from BOCK's Kreuterbuch. VALERIUS owed much to the work and inspiration of his father EURICIUS CORDUS; both father and son did his part for the advancement of science by

fighting against age-old superstition and bigotry during the rebirth of interest in intellectual work. It is difficult to say who was greater — the father in his struggle to plant new ideas and to inspire his son, or the short-lived youth.

The herbal of VALERIUS CORDUS published posthumously by GESNER in 1561 is important because it contains not only medicinal plants, wild or cultivated in Germany and Italy, but many foreign woods, barks, fruits, and resins acquired from other countries. CORDUS wrote his "Historia Plantarum" in Latin. His descriptions of plants were more accurate than those of any of his contemporaries, and relied less on the descriptions of the botanists of antiquity.

One of the most meritorious and noteworthy herbals of the 16th century was the De Historia Stirpium of LEONHARD FUCHS (1501-1566). Superior to his contemporaries in the matter of scholarship, FUCHS made himself eminently useful wherever he went. He studied medicine at the university of Ingolstadt and was later appointed professor of medicine. Becoming physician to Margrave GEORGE OF BRANDENBURG, he distinguished himself by his successful treatment of successive epidemics of the plague. Later he returned to the professorship in the university of Ingolstadt, but his stay was short, because he had meanwhile embraced the Lutheran faith. Within less than a year he withdrew and rejoined the Margrave of Brandenburg, soon left that position, partly because of the reappearance of the plague. In 1535 he was appointed professor of medicine in the newly organized Protestant university of Tübingen, and although he was subsequently offered attractive positions elsewhere, FUCHS remained at Tübingen for the remaining 31 years of his life.

FUCHS was primarily a medical botanist. There was nothing of the plant anatomist or physiologist about his work. His idea of the flower in general is similar to that given by THEOPHRASTUS. He distinguished two kinds of flowers, the leafy and the capillary, but regarded both as being united in flowers like the rose. His definition of a calyx was, "It is a kind of bag within which at first the flower, and, after that, the seeds are enclosed". He arranged the plants in the De Historia Stirpium alphabetically by their Greek names, hence we find no attempt at classification. In spite of these limitations the Historia which he produced, perhaps as a recreation from his professorial and medical work, commands admiration. The illustrations were made by two artists and the cuts by the best engraver in Strasbourg. The beautiful work contained about 500 artistic plates, excelling even those of BRUNFELS. The original edition written in Latin and published in 1542 was followed the next year by an edition in German augmented by six plates.

FUCHS listed and described many indigenous plants which are not found in BRUNFELS. New introduced plants were also listed and accompanied by figures. (*Triticum turgidum, Zea Mays* (fig. 10), *Ribes rubrum, Phaseolus vulgaris,* and *Tagetes patula*). Therefore it is apparent that FUCHS considerably augmented the list of European plants. The first edition of FUCHS' herbal contained pictures of 511 plants. FUCHS did not often name the localities in which the plants grew, but those he does mention are mostly in the vicinity of Tübingen.

FUCHS was more of an industrious compiler of information about plants than a botanist who was interested in investigation of plants, but so well did he succeed in his work of compilation that

FIG. 10. — Maize, *Turcicum frumentum* (Türckisch Korn), from FUCHS' New Kreüterbuch, 1543. One of the earliest figures of maize in a European book.

he laid a solid foundation for subsequent research. He enjoyed the study of plants as such, but his heavy duties as a physician and professor of medicine compelled him to restrict his energy to the compilation of medicinal and edible plants. His work gives evidence that, in spite of his attitude of reformation, he was still

imbued with a belief in the supreme authority of DIOSCORIDES. For him, the word of DIOSCORIDES was final, nothing should be added or taken from it.

REMBERT DODOENS (1517-1585) was another medical botanist who in 1554 published an important herbal, Cruydeboeck, utilizing many of the wood blocks from the octavo edition of FUCHS. The book was translated into English and published with some additions by HENRY LYTE under the title of A Niewe Herball (1578). DODOENS published in 1583 a larger work, Stirpium Historiae, in which he described many of the plants of the Netherlands which had not previously been studied and attempted a scientific arrangement of plants.

FIG. 11. — The bulbous iris (*Iris bulbosa*) from CLUSIUS' edition of DODOENS' Cruydt-Boeck, Antwerp, 1644.

CAROLUS CLUSIUS (CHARLES DE L'ECLUSE 1526-1609) deserves attention not only for his writings, but also for his career. He was a native of Arras and began his studies at the university of Louvain. After brief sojourns at Marburg, Frankfurt, Strasbourg, and Lyons, he entered the university of Montpellier in 1551, where he became interested in the study of botany. He obtained his degree in medicine in 1553, then travelled through Piedmont and Savoy, Geneva, Basel, and Cologne to Antwerp, arriving just after the Cruydeboeck of DODOENS had come from the press. His first important accomplishment was the translation of this herbal into French (1557). His first important original work was Rariorum aliquot stirpium per Hispanias observatarum . . . (1576) in which he described plants seen on a trip to Spain and Portugal.

Converted to Protestantism by MELANCHTHON, CLUSIUS was ostracized by many of his influential and wealthy patrons for his religious tenets. While directing the Botanical Garden in Vienna he introduced many plants previously unknown to Europe, among them, the white potato from South America. In every way he

extended the botanical horizons of his time; by his travels, by the introduction of exotic plants, and by his superb powers of observation.

The first Englishman to make a distinctly important contribution to botany was the versatile WILLIAM TURNER (?1515-1568). The appearance of his herbal marks the beginning of serious botanical work in England. He was prompted to undertake botanical work because of the imperfections of the Grete Herball, which was often inaccurate in plant descriptions and perpetuated moreover many medieval superstitions concerning plants. Libellus de re herbaria novus (1538) was a small book in which TURNER published the names and descriptions of many British plants and included the localities in which they had been found.

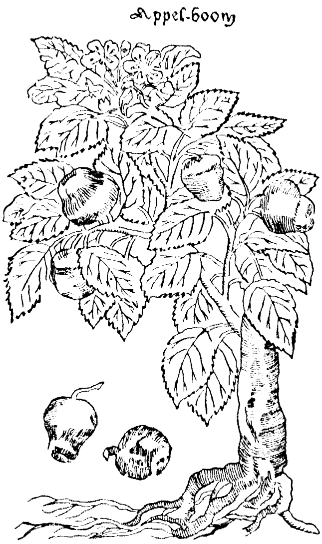


FIG. 12. — Apple tree (appelboom) and fruits. DODOENS' Cruydt-Boeck Antwerp, 1644.

TURNER embraced the reformed faith at Cambridge and became an ardent preacher of the new doctrines. He left the University in 1540 and travelled about England, but his religious beliefs brought him into disfavor with church dignitaries, and led to imprisonment and later to exile from England. During his enforced visit to the continent TURNER improved his time by travel and study. Having studied under GHINI at Bologna, he took a degree in medicine. He visited GESNER in Switzerland and corresponded with FUCHS, from whom he obtained the use of the wood-blocks which had been used in the publication of FUCHS' Herbal of 1545. He thus learned more from the botanists of the continent during his exile than he could have learned if he had remained unperturbed in England. He was requested to return to England to take the post of physician to the Duke of Somerset who was also greatly interested in the study of botany and who had a large garden.

In 1551 he published the first part of his Herball, followed by the second in 1562, and the third in 1568. It was entitled "A new

Herball, wherein are conteyned the names of Herbes . . . with the properties, degrees, and natural places of the same, gathered and made by WYLLIAM TURNER, Physicion unto the Duke of Somersettes grace". The work is reminiscent of BRUNFELS in the attempts to describe what he actually saw. He said in defense of the work, "I wente into Italye and into diverse partes of Germany, to knowe and se the herbes my selfe". He wrote that herbal in English in order to aid the apothecaries who, he said, did not know Greek or Latin and who needed more knowledge of the plants they used.

The following excerpt from the herbal casts an interesting light on the man — his caution, and his attempt to compare what different authors had said. In conclusion he states that he has seen only dried specimens, his own judgment therefore may not be entirely reliable. Here are marks of a good scientist:

> Amaranthus is not the same herbe in Galene/that is in Plinye/for their descriptions of Amaranthus are diverse & differing. Amaranthus of Pliny as he writeth him selfe/ is rather a purple eare then a floure . . . It is called in English/ purple velvet floure/ or flour amour. The herbe which is named in Dioscorides Elichrison/ is also called of Galene Amaranthus/ and thus it is described of Dioscorides. Heliochrison hath a litle whyte braunche/ grene/ streight & stronge and narrowe leaves like unto Sothernwod/ certaine spaces goyng betwene the leaves/ the top is al yelowe/ and is full of rounde knoppes lyke unto drye berryes/ the roote is verye small . . . Matthiolus sayth that this herbe groweth much in Hetruria/ I never sawe it growe as yet but onlye drye . . .

The plants are arranged alphabetically since no thought was then given to plant relationships. TURNER knew more plants than one might think possible and gave to many the English names they bear. With an apparently inborn zeal for reformation TURNER swept out many of the old superstitions about plants.

The influence of gardening on the development of botany may be seen in the work of JOHN GERARD (1545-1612) who had an unusually extensive private garden either in Fetter Lane or Holborn in London and had charge as well of other gardens. GERARD published (1596) an account which contained over 1033 species of the plants growing in his garden. This account, entitled Catalogus arborum fruticum ac plantarum tam indigenarum quam exoticarum, is a notable example of the development of gardening in the 16th century showing the extent to which plants, regardless of their utility, were assembled from many parts of the world.

In 1597 GERARD published his greatest work, the Herball, or Generall Historie of Plants, illustrated with over 1800 wood-cuts of plants, only 16 of which were original and quite inferior to the others. One of the most interesting original illustrations is that of the potato, although it was published over the incorrect and misleading name "Potatoes of Virginia — Battata Virginiana sive Virginianorum et Pappus". This error was perpetuated for some time, but eventually it was ascertained that the potato did not come from Virginia, and that it does not belong to the species *Ipomea batatas*. GERARD's portrait bearing the date of 1598 holding a flowering shoot of the potato was inserted at the end of the preface of the herbal. The prominence thus given was perhaps an indication of his esteem for the potato.

Though this book is known as GERARD's Herball and bears his name, it is not an original piece of work, and the history of its

publication does not reflect very great credit on its author. GERARD seems to have been gullible with respect to many plant myths and to have appropriated the work of others without properly acknowledging his sources. The edition of the Herball published in 1633 was greatly improved by THOMAS JOHNSON, a London apothecary, who corrected many errors and illustrated it with PLANTIN's wood-cuts.

FIG. 13. — *Caltha palustris maior* (The great Marsh Marigolde). "Marsh Marigold hath great broad leaues somewhat round, smooth, of a gallant greene colour, slightly indented or purlde about the edges, among which rise vp thicke fat stalkes, likewise greene: wherupon do growe goodly yellow flowers, glittering like gold, and like to those of Crowfoote, but greater: the roote is small, composed of verie manie strings . . .". From GERARD's Herball, p. 670 (1597).

Another herbalist, very different from the others, who also made important contributions to botanical science was ANDREA CESALPINO (1519-1603) of Arezzo. As a child he hated study and drill work; his parents and teachers, finding punishment to be of no avail, finally despaired of ever educating him, but being left to his own devices, he astonished them by becoming an outstanding scholar. He eventually went to Pisa and studied medicine and botany under GHINI. In 1555, he succeeded ALDROVANDI as the director of the botanical garden at Bologna and two years later he became professor of botany there, occupying also the medical chair. In 1592 he went to Rome, as physician to Pope CLEMENT VIII, and also as professor of botany at Sapienza University.

De plantis, the most famous work of CESALPINO, appeared in 1583. It consists of sixteen books, fifteen of which describe some fifteen hundred plants, and one, the first, only thirty pages long, states his theory of botany in concise terms and is more valuable than the other fifteen combined.

In addition to his book, his herbarium, consisting of 260 pages with 768 well-mounted plants with their names in Latin and in Italian dialect, is still in existence.

His approach to botany was very different from that of any of his contemporaries, and indeed is not found again until the time of LINNAEUS two centuries later. He was essentially a philosopher, of the Aristotelian school, and was seeking a system of plant classification based on philosophical reflections rather than on the realistic utilitarian approach of most physicians and pharmacologists.

In substance, CESALPINO showed on philosophical grounds that there must be classification, and proceeded to carry out this classification mainly on the basis of character of fruits and seeds, but he considered also the period of viability of the plant, the situation of the radicle, the form and nature of the roots, and the presence or absence of flowers and fruits. Many of his ideas on plant physiology and anatomy are quite as interesting as they are fallacious. He had anticipated the discovery of the circulation of blood in animals and sought a similar function in plants. The seat of this function, or the "plant soul", was supposed to be the point of junction of the root and stem. As he considered plants to be an imperfect imitation of the animal kingdom, he carried his analogies further. The pith corresponds to the spinal cord and is the source of heat energy. He said further:

> As the nature of plants possesses only that kind of soul by which they are nourished, grow, and produce their like, and they are therefore without sensation and motion in which the nature of animals consists, plants have accordingly need of a much smaller apparatus of organs than animals. But since the function of the nutritive soul consists in producing something like itself and this like has its origin in the food for maintaining the life of the individual, or in the seed for continuing the species, perfect plants have at most two parts, one part called the root, by which they procure food; the other by which they bear fruit, a kind of foetus for the continuation of the species; and this part is named the stem in smaller plants, and the trunk in trees.

With all his emphasis on seeds, he denied the existence of sex in plants. Leaves, he believed, functioned in nutrition, but more importantly as protection for the fruits, and were produced from the bark. He believed that seedless plants were "bred of putrefaction".

Many of his observations are more constructive than the foregoing. He recognized a definite pattern of phyllotaxy, and, in anticipation of GOETHE, believed that flowers had arisen from leaves. Of fruits, he says:

> As the final cause of plants consists in that propagation which is effected by the seeds, while propagation from a shoot is of a more imperfect nature, so the beauty of plants is best shown in seed-production; for in the number of parts, the forms, and varieties of seed-vessels, the fruit-bearing stage shows far more adornment than the unfolding shoot.

He clearly stated that some plants have two seed-leaves, while wheat has but one, and sometimes these leaves sprout above the

ground and nourish the seedling, while others are used up before the seed sprouts. CESALPINO exerted a more profound influence upon botanists of the following century than any of the 16th century writers. His importance has been ably and critically discussed by SACHS.

JOHANN BAUHIN (1541-1613) who was at one time a pupil of FUCHS, later of ALDROVANDI at Bologna, described about five thousand species in a clear and accurate manner, taking into consideration all the organs and properties of the plant as well as its ecology.

Meerfichten. Pinus Maritima. I.

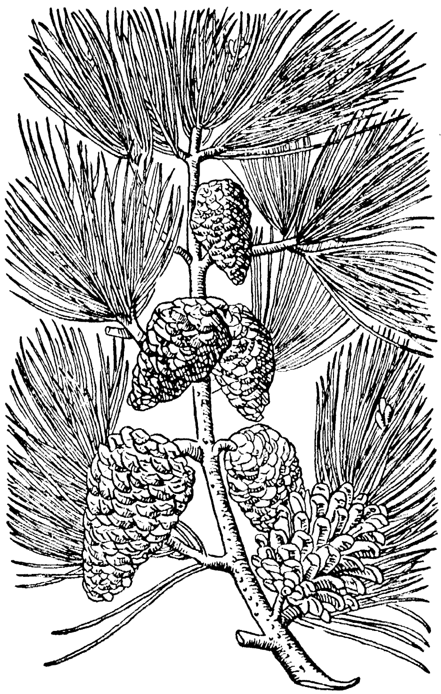


FIG. 14. — *Pinus maritima* from MATTHIOLI and CAMERARIUS, New Kräuterbuch (VERZASCHA Compiler). — "Die Fichten /so bey dem Meer wachsen / sind zweyerley / wie aus dem Gemalde / so alhier nachgesetzt augenscheinlich zu erkennen. Diese Baume haben langer / glatter / schoner zirbeln / lindere blatter / stamm und rinden".

His important work was his Historia plantarum universalis in three volumes. His illustrations consist of 3,577 wood-cuts, taken largely from FUCHS, but the paper and print are of such poor quality that they are of little value.

KASPAR (1560-1624), the younger brother of JOHANN BAUHIN, was a more important botanist. He was not strong, and his family planned for him to enter the ministry, but he, like his father and brother, insisted on studying medicine. After having been taught by his father, he entered the University of Basel at the age of sixteen. When the plague threatened, he went to Padua. His wealthy god-father in Holland died about this time, leaving him an

extensive library and a considerable fortune, of which BAUHIN made good use. He spent two years in Italy collecting plants, then travelled over much of France and Germany, studying at Paris, collecting and studying plants everywhere, and becoming acquainted with other botanists. In 1580 his father's illness recalled him to Basel, and the following year he received a degree to teach botany and anatomy.

His Phytopinax (1596) described 2700 species, beginning with the *Graminaceae* and ending with *Papilionaceae.* A portrait of the author at the age of twenty-nine appears in this book.

The Prodomus theatri botanici (1620) contains a terse and orderly diagnosis of 600 plants which he believed to be new, including the potato, to which he gave its present name of *Solanum tuberosum.* This book contains 140 good illustrations, while the Pinax is not illustrated. His greatest work was a much-needed synonymy of plants, giving all the names by which different writers had designated each plant. This book to which he devoted 40 years was his Pinax theatri botanici (1623) containing 6000 species. He applied mostly binomial names, and attempted a classification by natural affinities proceeding from the grasses through the lilies, dicot herbs, and shrubs and trees. SACHS evaluates the work as follows: "it is still indespensable for a history of individual species. No small praise to be given to a work that is more than 250 years old". BAUHIN's method was most valuable because he discarded all the old ideas of medical superstition and sought a classification according to natural affinities, but he was singularly oblivious to the importance of flowers and fruits.

Though JOHANN and KASPAR BAUHIN never collaborated, there is a genus of lianas or "turtle-ladders" which PLUMIER dedicated to them, calling it BAUHINIA. It includes 150 species, the most striking of its features being the twin-lobed leaves, symbolic of the two brothers.

Herbalists in the Orient:- This brief account of herbals and their writers will conclude with a mention of two celebrated Chinese herbals of that period, which, although comparatively little known in the Occident, have been of tremendous importance in the Orient. These works, like their European counterparts, were highly esteemed by the laity as well as the scholars and were frequently republished. They constitute important source material for the history of the utilization of wild plants and their domestication. Many illustrated herbals which embodied the results of plant collectors and cultivators, were published in China.

The Chinese people have for centuries lived close to the soil and have felt the necessity of securing every plant that could possibly serve for human food. Fortunately, the Chinese flora is rich in species. After centuries of agro-botanical work the Chinese people have a vastly larger number of crop plants than the farmers of Europe or America. Their experiences have also given them knowledge of many medicinal plants which otherwise would have remained unknown. To a considerable extent the Chinese make no sharp distinction between food and drug plants; practically all of the food plants are used in their materia medica.

CHOU WANG HSIAO who published in 1406 a remarkable herbal illustrated with wood-cuts of high artistic quality (fig. 15) was

an imperial prince, son of the first Ming emperor, HUNGWU, who reigned from 1368 to 1398. Prince CHOU, being painfully aware of the terrible suffering of the people during the recurrent famines, engaged in the laudable enterprise of increasing the food supply.

He had a checkered career, serving part of the time in high official posts and part of the time being in disgrace or banishment. From 1382 to 1400 he is said to have lived on his estates in Honan province, where he secured from farmers and hermits 400 or more kinds of plants supposed to be suitable for food in time of famine. These he set out in a garden where he personally observed them, drew up descriptions, and had artists make drawings of them. He then arranged these plants in groups according to the edibility of their leaves, fruits, blossoms, roots, etc., and published the work under the title Chiu huang pên ts'ao or "Relieve Famine Herbal"

FIG. 15. — Illustrations from the Chinese "Relieve Famine Herbal", Chiu huang pên ts'ao written in 1406. Left: Li tzu shu, the Li plum, *Prunus communis* Huds. Right: Hsüan ts'ao hua, blossoms of *Hemerocallis* (probably *Hemerocallis fulva* L.). Reproduced by J. S. YIP.

with a preface by his friend and helper, PIEN T'UNG, dated 1406, in which year it was probably printed.

In this remarkable book Prince CHOU briefly described and figured 414 species of plants, of which only 138 had been discussed in previously published herbals, and 276 were here described and figured for the first time. Furthermore this excellent herbal antedated by 69 years the first European printed book containing figures of plants (KONRAD OF MEGENBERG's Puch der Natur). As the Chiu huang pên ts'ao is primarily concerned with wild growing plants that can be used for food in time of famine, it is not limited to plants known to have medicinal virtues. It is, in fact, a valuable early treatise on Chinese botany, and because of its excellent illustrations is an outstanding work in its class.

The "Relieve Famine Herbal" must have become a very popular work in China and was worn out by frequent use as is evi-

denced by its extreme rarity. It is known that it was reprinted in 1526, 1555, and 1566.

The other herbal, better known in Europe since numerous translations have been made, is the first treatise of this kind in which botanical subjects were critically treated. It is the Pên ts'ao kang mu (1590) written by LI SHI CHEN. It contains 52 chapters enumerating the 16 divisions and the 62 classes under which the whole matter is arranged. The section on plants contains 5 of the 16 divisions, namely:

I. HERBS

Ginseng (*Jen-Shên*), liquorice, mint, *Hibiscus, Iris*, rhubarb, *Aconitum, Acorus, Typha*, ferns, mosses, etc.

II. GRAINS

Hemp, barley, wheat, buckwheat, sesame, rice.

III. KITCHEN HERBS

Leeks, garlic, onion, carrot, spinach, sweet potato, beets, melons, mushrooms.

IV. FRUITS

Plum, apricot, peach, apple, orange, walnuts, dates, pepper, tea.

V. TREES

Thuja, cedar, pine, camphor, *Sterculia*, elm, willow.

It may be said that LI SHI CHEN was the first and the last critical writer on Chinese natural science and that he has never been rivalled by other authors. He spent 30 years on the work and consulted about 800 authors. As an example of the value of this herbal, one may note that it contained a notice and illustration of maize. LI's detailed description and crude figure leave no doubt as to its identity. This shows that maize had then become an important food plant in parts of China. The assumption that maize may have been introduced into China in pre-Colombian times is disproved by the absence of any notice of this cereal from all Chinese herbals published prior to the discovery of America.

Botanical explorations:- Medieval Europeans seldom travelled far, and the Orient was not in their pathway. Few were courageous enough to penetrate countries about which fabulous and terrifying tales were told, consequently commerce between Europe and China was left to foreign traders. The travels of the Venetian, MARCO POLO (c. 1250-1324), were therefore unique and the narrative which he subsequently wrote gave Europeans almost the only knowledge they possessed of the Orient for centuries (fig. 7). He mentioned, but gave no descriptions of such Chinese plants as wheat, rice, peaches, quinces, ginger, bamboo, etc., which were generally connected with the economic and social life of the people. POLO spent about 24 years chiefly in China, where, for three years he administered a whole province.

The knowledge of geography might have been immensely promoted by POLO's accounts of oriental countries, but the majority of the people accused him of gross exaggerations and outright fabrications. Subsequent travels have, however, established the accuracy and veracity of his narrations.

IBN BATUTA (1304-1378) of Morocco visited countries of the Near and Far East in the 14th century and left a noteworthy narrative in which his experiences are recorded. He was primarily interested in the religious and social customs of the people, writing

always from the standpoint of the theologian. Intending only to make a pilgrimage to Mecca and other cities revered by Mohammedans, eventually he visited Anatolia, Persia, India, China, and northern Africa. IBN BATUTA discovered nothing of great botanical importance. His records of plants are in terms of food and raiment. But he gave a permanent and colorful record of the life of the Orient. The absence of any real spirit of inquiry on the part of IBN BATUTA is a commentary on the scientific spirit of his time, rather than on that of the man. The sudden change in attitudes in the following centuries is one of the characteristics of the Renaissance.

We have already seen that some of the European botanists were interested in travelling in search of new plants. CLUSIUS found many things of interest in southwestern Europe and when he later directed the botanical garden in Vienna, he obtained and cultivated many extra-European plants.

NICOLAS MONARDES (1493-1588) was an eminent physician in Seville, who, although he never visited the Americas, wrote two volumes on their natural products which kindled lively interest in the New World plants. The first was published in 1569, the second in 1571. Both were so popular that he combined the two and published them as one volume in 1574.

The title of the combined work was, "Primera y segvnda y tercera partes de la historia medicinal de las cosas que se traen de nuestras Indias Occidentales que siruen en medicina" (Seville, 1574). MONARDES was supremely enthusiastic about the additions to materia medica obtained from the New World. He wrote unhampered by too many facts and, having an apparently credulous mind, wrote in a fashion which makes diverting reading. If half that he wrote were true no one need have been ill for long. He shows many evidences, however, of a real interest in science and experimented on his patients. He sometimes concluded his discussion of some new herb by saying that this was what he understood from those who brought it to Spain, and that when he had had time to learn more of it, he would write of its use.

The esteem in which the writings of MONARDES were held is shown by the promptness with which they were translated into other languages. JOHN FRAMPTON, a British merchant who had been in Spain, translated and published the combined work in 1577; three years after it was published in Seville. The arresting title of the English edition was "Joyfull Newes out of the Newe Founde Worlde, written in Spanish by NICHOLAS MONARDES, physician of Seville, and Englished by JOHN FRAMPTON, Merchant, Anno 1577". FRAMPTON published a second and enlarged edition of this work in 1580. The knowledge of the new medicines was disseminated by CLUSIUS who translated MONARDES' work into Latin and first published a part of it in his Exotica.

The wealth of material brought by explorers and their reports about other plants in the Americas doubtless inspired PHILIP II of Spain to send a competent man to explore and investigate some of the fantastic stories about the products of that wild, luxuriant country. His Majesty doubtless knew the innate propensity of sailors to go beyond the facts when descanting upon matters of a remote and seldom visited land. He therefore commissioned his physician, FRANCISCO HERNANDEZ, to embark on what was probably the first botanical expedition sent out by a government,

and to obtain information, not only about plants and their uses, but also about the antiquities and political conditions of the countries visited.

HERNANDEZ sailed from Spain in 1570 for Mexico bearing the title of Protomedico of the Indies and taking his son as assistant. It was fortunate that he was commissioned to explore a country as rich in plants as Mexico and where the inhabitants had done so much botanical and horticultural work through many centuries. HERNANDEZ' enthusiasm may well have been kindled by the discovery that the Mexican people had an empirical materia medica of many years standing and well-organized botanical gardens. There were parts of the new world where his success would have been more difficult. He proceeded to study the plants and their medicinal properties, making experiments not only on patients in hospitals, but also upon himself. While on an exploring trip in Mechoacan he narrowly escaped death as a result of an experiment with the latex of "chupirre". Native physicians worked with him in testing the effects (on patients!) of native drugs and reported on the results of their tests. With indifferent success HERNANDEZ also wrote descriptions of the plants from which the products were obtained. It is difficult in many cases to determine what plants he was discussing because both the descriptions and the drawings are vague in respect to important matters. The book is, however, of great interest as an early American herbal, though it failed to play its deserved role in the development of botany.

PHILIP II had assigned a period of five years for HERNANDEZ' exploration and appropriated funds accordingly. As often happens, the funds ran short before the work was done, and HERNANDEZ suffered acute financial embarrassment. He had completed 16 folio volumes on the plants by the end of 1575, yet remained two years longer without salary from the king before returning to Spain.

The results of this first official scientific expedition for the study of plants are of great historical interest because they assembled and conserved a mass of information on ethno-botany which otherwise would have been lost. The lack of scientific spirit in the work may be due partly to the fact that it was not published until long after HERNANDEZ' death and partly to the fact that only a fraction of it was eventually published by reason of many vicissitudes. The best known edition was published in Madrid in 1790.

The records of plant introductions into Europe are not complete in all respects, but there is much evidence that the work of men like MONARDES, OVIEDO, and HERNANDEZ resulted in bringing in many plants, of which only a few may be briefly mentioned here.

Tobacco was first carried to Europe by a soldier returning from Florida and imprisoned in Portugal. JEAN NICOT, French ambassador to Portugal at the time, obtained from the prisoner some of the seeds and grew plants in his garden. After seeing them flourish there, he sent some powdered snuff to King FRANCIS I and to CATHERINE DE'MEDICI, in whose court it obtained a great vogue for use in headaches. The royal recommendation influenced its subsequent diffusion. In 1635, however, LOUIS XIII of France interdicted its use except on prescription of a physician; it was not many years, therefore, before smoking began to supersede the

remedial use of tobacco on the continent. Sir JOHN HAWKINS probably carried it to England in 1565 and it was being used for smoking by Sir WALTER RALEIGH by 1573, probably after a second introduction by DRAKE.

By other routes the Europeans received products like guiacum, balsam of Peru, sarsaparilla, sassafras, cinchona, capsicum, ipecac, and copal.

As MONARDES said (FRAMPTON's translation), "as there are discovered new Regions, new kingdoms, and new Provinces by our Spaniards so they have brought unto us new Medicines, and new Remedies, wherewith they do cure many infirmities, which, if we did lack them, would bee incurable and without any remedie".

European missionaries in the Orient began to communicate information about Chinese plants in the 16th century. MARTIN DE HERRADA, an Augustinian monk, spent three months in 1575 at the port of Ts'uan chou fu in the province of Fu kien. His observations were published by a brother monk, J. GONZALEZ DE MENDOZA in a book entitled "History of the great and Mighty Kingdom of China" (Rome, 1585). While the information about plants in the book is brief, it is important. After mentioning the excellence of the chestnuts and melons, he reports that "The Chinese have a kind of plum, that they call leechias, of an excellent, gallant taste". Here we have the first known mention of the Litchi (*Nephelium litchi* Camb.) by a European writer. HERRADA also reported that the cereals cultivated in China were wheat, barley, millet, and maize. The mention of maize is important because it shows that the Spaniards who took it to the Philippines at an early date were instrumental in introducing the plant into China.

The four centuries which have been considered in this chapter cover a period of great importance in the development of botany. During this time a true revival of the scientific spirit took place, not only in regard to the plant sciences, but also in regard to all activities. The reawakening showed itself in many different ways according to the circumstances and training of the men who devoted their lives to some phase of science. The period considered was characterized by an immense activity in the accumulation of knowledge about plants. The motive for collecting much of this information was the interest in medicinal herbs. The world found plants in the fields and woods which could be used for healing many infirmities. People therefore went to extremes in looking for some curative property in every plant. Unfortunately, they were often disappointed. It was necessary, however, to have accumulated a considerable body of information before any intelligent work could be started on a scientific discovery of the principles of plant life. A great widening of the horizon of men's lives occurred with respect to the vegetable world. Starting first in their own towns and countrysides and ending eventually in China, India, and in the newfound world of America, they found a wealth of new material.

REFERENCES:

ARBER, A. (1912): Herbals. University Press, Cambridge.

BARTHOLOMAEUS ANGLICUS (1907): Mediaeval lore from BARTHOLOMAEUS ANGLICUS, by R. Steele (Ed. and Comp.). Chatto and Windus, London; Luce, Boston.

GREENE, E. L. (1909): Landmarks of botanical history, Part I - Prior to 1562 A.D. Smithsonian miscellaneous collections, Part of Vol. 54.

HAWKS, E. (1928): Pioneers of plant study. Sheldon, London; Macmillan, New York and Toronto.

MEYER, E. H. F. (1854-57): Geschichte der Botanik. Gebrüder Bornträger, Königsberg.

MONARDES, N. (1577): Ioyfvll nevves out of the nevve founde worlde . . . Englished by IHON FRAMPTON. London, W. Norton. (Transl. of his "Primera y segvnda y tercera partes de la historia medicinal . . ." Sevilla, A. Escriuano, 1574).

ROHDE, E. S. (1922): The old English herbals. Longmans, Green, London, New York, etc.

SACHS, J. VON (1890): History of botany (1530-1860) . . . authorized transl. by H. E. F. GARNSEY . . . Rev. by I. B. BALFOUR. Clarendon Press, Oxford. Original German ed., 1875.

SARTON, G. (1931): Introduction to the history of science, Vol. 2. Publ. for the Carnegie Institution of Washington by the Williams & Wilkins Company, Baltimore.

SCHWERTNER, T. M. (1932): St. Albert the Great. Bruce, New York, Milwaukee, etc.

SPRAGUE, T. A. (1928): The herbal of OTTO BRUNFELS. Linn. Soc. London, Journal 48:79-124.

—— —— and E. NELMES (1931): The herbal of LEONHARDT FUCHS. *ibid.* 48:545-642.

—— —— and M. S. SPRAGUE (1939): The herbal of VALERIUS CORDUS. *ibid.* 52:1-113.

STRUNZ, F. (1926): ALBERTUS MAGNUS, K. König, Wien und Leipzig.

SWINGLE, W. T. (1930): Notes on Chinese accessions on medicine and materia medica . . . (*In* U.S. Library of Congress. Report of the librarian 1929-30:p. 368-379).

Chapter VI.

THE SEVENTEENTH CENTURY.

The importance of the scientific developments in the seventeenth century has often been emphasized by historians and humanists. Science, which had been wakened in the sixteenth century, began to show activity in the seventeenth - an activity which eventually changed man's affairs. New systems of philosophy were formulated by men like DESCARTES, HOBBES, SPINOZA, LEIBNITZ, and NEWTON. Men realized that the new knowledge which was being acquired needed organization and the inadequacy of facts handed down from the past and the importance of experimentation were keenly realized about the same time by men of that generation in many countries. These men played the part of reformers. They encountered no end of opposition and sometimes left scanty records of their studies, but they broke roads on which others travelled.

At the beginning of the seventeenth century, astronomy had probably advanced more than the other sciences, due largely to the discoveries made by the use of the newly invented telescope in the hands of men like GALILEO. We shall see that a great advance in the biological sciences also followed the invention of the microscope during this century. Knowledge of the living world grew by leaps and bounds when precise observations were possible.

Biology in the seventeenth century received a great impulse from HARVEY's discovery of the circulation of the blood (1628) and BORELLI's attempt to give a mechanical explanation of life phenomena (1685).

Scientific societies and scientific academies were organized to encourage science and to afford their members an opportunity of presenting the results of their investigations. These institutions performed important functions in many ways since many of the leading scientists of the seventeenth century were not in universities. Some of the societies were chartered by sovereign powers, thereby giving them a definite and more enduring status. In Italy the Accademia dei Lincei was organized by Duke FEDERIGO CESI in 1601 (dissolved in 1657) and the Accademia del Cimento by the MEDICI brothers, Grand Duke FERDINAND II and LEOPOLD in 1657. The Royal Society of London (1662) was inspired by BACON's New Atlantis. The Académie des Sciences (1666) in France was chartered by LOUIS XIV whose liberal offers had attracted scholars from all quarters. The Berlin Akademie der Wissenschaften (1700) was founded by LEIBNITZ.

A revival of interest in natural philosophy:- JOACHIM JUNG (1587-1657) gave an impetus to botanical study which continued for many years after his time. It was said of him that "he was a philosopher of the type of CESALPINO, but without Aristotelian obsessions". Born in Lübeck, he obtained at the age of 22 a professorship in mathematics in Giessen, and received the degree of doctor of medicine in Padua in 1618. While at Padua, he

undoubtedly became conversant with the ideas of CESALPINO who had been dead only 15 years. He settled in Hamburg in 1628 where he remained the rest of his life.

JUNG's significance in biology lies in his philosophical concepts of living organisms. For the first time since ARISTOTLE and THEOPHRASTUS the principles of botany had become a subject of interest. JUNG's writings contained almost nothing on experimental work, especially on the subject of nutrition. Other concepts rested, not on new observations, but on the interpretation of existing observations and on plants already known.

JUNG described no plants, nor founded any system of classification, but devoted himself to morphological problems which might serve as a basis for such a system. He departed in several particulars from CESALPINO, *e.g.*, discarding the classification of plants into trees and shrubs. He thought that the leaf was an important character for classification, but that other organs like thorns, color, odor, taste, etc., were entirely fortuitous. Discarding the ancient classes of trees, shrubs, and herbs, he reduced all to the same terminology. He was interested in the general parts of the plant and decided that the important parts were the root and the stem; accordingly, the trunk of the tree and the culm of the grass were stems. In this way he expressed the idea which permeated the entire work, "All parts which in their inner nature are alike must bear the same name regardless of their shapes". He considered that the general parts of a complete plant were root, stem, leaf, flower, fruit, and seed. He definitely excluded the "cordus" of ARISTOTLE which was supposed formerly to provide a junction between stem and root. A complete flower was said to be composed of flower leaves, dust leaves, and style, which JUNG designated as folium, stamina, and stilus. He saw the difference between dorsiventral flowers (*Salvia*) and radial flowers (tulip and rose). He was undoubtedly one of the first of modern botanists to study morphology apart from taxonomy. His thorough comprehension of the nature of the plant vitalized the subject of botany and started a much needed reformation. There is no proof that JUNG possessed a herbarium although he knew from his experience in Italy the usefulness of collections of dried plants.

After considering the functions of plants, JUNG came to the following conclusions: (1) The plant possesses no intelligent soul which enables it to distinguish advantageous from harmful nutrients; (2) The mouth of the root is so devised that it does not allow all saps to enter, *i.e.*, the pores of the root are closed and impermeable to a given substance in one species, but open and permeable in another; (3) Plants, like other living things have excretions which are given off to flowers, leaves, and fruits, even as resins, and fluids.

JUNG's effectiveness was partly lost because he personally published nothing of his botanical work; our knowledge of it is obtained from two volumes later published by his students. The two works are entitled "Doxoscopiae physicae minores" (1662) and "Isagoge phytoscopica" (1678). The first work is not purely botanical, but contains five fragments which treat of the establishment and recognition of species, the homologies of organs, and the life of the plant. This last division which treats various physiological problems has already been mentioned.

The "Isagoge" is a "Handbook of Botanical Study" containing theoretical considerations of plants, but formulating no system of classification. Although it contained only 46 quarto pages, it can be regarded as a pioneer work in botany because it evolved a terminology with a clearness of perception which has been excelled only by LINNAEUS. The following quotation illustrates its style: "A leaf is that which stretches out from its place of attachment in height and length so that the surfaces of the third dimension are dissimilar to one another; it is the leaf's inner surface which is differentiated from the outside". He was undoubtedly one of the first botanists of modern times to study morphology apart from taxonomy and his thorough comprehension of the nature of the plant vitalized the subject of botany. Notwithstanding the complex diversities of plants, JUNG discovered relationships and essential characters theretofore unperceived by his predecessors. With all his skill in detecting the nature of the plant, he held the opinion, prevalent at the time, that mosses and fungi were not "complete" plants, but were aborted plant foetuses. He started, nevertheless, a much needed reformation in botany.

Systems of plant classification:- JOSEPH PITTON DE TOURNEFORT (1656-1708), who was born at Aix in Provence, introduced ideas of plant classification which were distinct advances, although he failed to comprehend the sexuality of plants. In his opinion the morphology of the flower and fruit was the proper basis for classification of plants and he opposed the idea that the root, stalk, and leaf could provide reliable characters. He revived the concept of genera and species which had been formulated by KASPAR BAUHIN, but placed the chief emphasis on the genus. Perhaps his most valuable contribution to botany was the start he made in working out a system of groups higher than genera, for example, presence or absence of a corolla, cruciform corollas, and so forth. It is true that he gave no names to these larger groups, and that his classification was highly artificial, but it was an expression of a valuable idea and maintained its position till the time of LINNAEUS. After having explored his native province, he was sent at the expense of the king to Spain, Portugal, the Grecian archipelago, the Black Sea, Asia Minor, etc. He published several botanical works including "Voyage du Levant" (1717).

ROBERT MORISON (1620-1683) was a Scotsman who made great additions to the knowledge of plant classification in the seventeenth century, although hampered by a nature that was inclined to be contentious and disputatious. On leaving college, he became embroiled in the troubles of the English Civil War and joined the Royalists against CROMWELL. After their defeat, he went to Paris, where he engaged in the study of botany under ROBIN, botanist to the King of France. In this undertaking MORISON was particularly successful and attracted attention to his ability as a botanist. The King's uncle, GASTON, duke of Orleans, appointed him director of his private garden at Blois, a position which he held from 1650 to 1660, when his benefactor died. The House of Stuart having been restored to the throne in England, CHARLES II invited MORISON to return. He accepted and was made Physician to the King, Royal Professor of Botany, and Director of the Royal Gardens. Owing to his fortunate situation, he was able to carry

on and finish a great deal of work. In 1669 he accepted the post of professor of botany at Oxford University, where he remained until his death.

MORISON's ideas were set forth in his Hortus Regius Blesensis (1669), which formed part I of his Praeludia botanica in which he gave the rudiments of his system of classification. His most important work was Plantarum historiae universalis Oxoniensis, Pars secunda . . . (1680), which described herbaceous plants. The first part of the Plantarum historiae, on trees and shrubs, was never printed. Some have doubted, said PLUNKENET, whether it was ever written, but there is reason to believe that it had been completed in manuscript form prior to his decease. MORISON's system was founded on the fruits and on the habits of the plants conjointly. For example, Class 1 was "Scandentes", Class 2 "Leguminosae", and so on.

MORISON has been censured for his arrogant and disputatious attitude toward other botanists. He implied that he had drawn all his information first hand from the study of plants and maintained the utmost silence respecting any assistance drawn from his predecessors; yet it was perfectly evident that he had drawn freely on CESALPINO, GESNER, and others.

If anything were needed to show that the age of the herbalists was over and that a new era in the study of plants had begun, we could point to the work of JOHN RAY (1628-1705). The greatest advance in plant classification in the seventeenth century was made by RAY, a man who exemplified the highest ideals of science, character, and scholarship. The system of classification which he founded was the basis for that of DE JUSSIEU and of DE CANDOLLE and had therefore an abiding influence on the development of botany.

The accounts of RAY's interesting life have been so frequently and so well given that the briefest notice will here suffice. He had a brilliant career as a student at Cambridge University. There he pursued theological studies and was ordained as a minister in 1660. He then held a fellowship in Trinity College, Cambridge. For conscientious reasons, he resigned the fellowship in 1662 and left Cambridge. For several years he travelled extensively in England and Scotland and on the Continent. The travel was made possible through his warm friendship with WILLUGHBY, a man who possessed a considerable fortune and was able to provide for all RAY's needs. RAY's love of the natural sciences, manifested from student days, asserted itself in several ways. His botanical excursions around Cambridge were gradually extended to cover England and Scotland. Eventually he travelled for three years over France, Holland, Germany, Switzerland, Italy, and other regions, studying the plant life as he travelled.

RAY's first publication was a modest catalog of plants growing in the vicinity of Cambridge, but in an appendix he stated tentatively his ideas on classification which were later developed.

His large three-volume work, Historia plantarum, was published between 1686 and 1704. The whole plant kingdom was divided into herbs and trees, exemplifying again the influence of the Greeks almost to our day on botany.

He divided the herbs into Imperfectae (algae, fungi, mosses, ferns — but these terms, however, did not have the same connota-

tion as in present-day use) and Perfectae, which were further subdivided on the basis of the cotyledon into 19 dicotyledonous and 3 monocotyledonous groups. Trees were divided also into monocotyledons and dicotyledons. This classification was not perfect by any means, but it expressed some important ideas. True, most of his classes had been previously named by botanists and were very unequal in extent, but they emphasized the importance of the flower and fruit for classification. The book in its second and subsequent editions was popular and its method was taught widely by some of the most eminent botanists on the Continent. In 1688 RAY published Fasciculus Stirpium Britannicarum, which was an enlarged edition of the catalog of English plants which he had published in 1670. On the eve of publication of this new edition, a dispute with his publishers arose which led to its appearance as a totally new work. He accordingly abandoned the alphabetical arrangement of the catalog and grouped the plants according to his own scheme of classification. This book which became very popular with the botanists of that period was, in fact, the basis on which the floras of England have subsequently been founded. It was simplified and made more generally useful than its two predecessors by its systematic arrangement and the reconsideration of generic characters of an increased number of plants.

The final system of RAY (taken from SACHS' *History of Botany*):

A. PLANTAE GEMMIS CARENTES (HERBAE)

(a) IMPERFECTAE

i—Plantae submarinae (chiefly Polypes, *Fucus*)
ii—Fungi
iii—Musci (Confervae, Mosses, Lycopods)
iv—Capillares (Ferns, *Lemna*, *Equisetum*)

(b) PERFECTAE

Dicotyledones (binis cotyledonibus)

v—Apetalae
vi—Planipetalae lactescentes
vii—Discoideae semine paposo
viii—Corymbiferae
ix—Capitalae (vi-ix are compositae)
x—Semine nudo solitario (*Valerianeae*, *Mirabilis*, *Thesium*, etc.)
xi—Umbelliferae
xii—Stellatae
xiii—Asperifoliae
xiv—Verticellatae (*Labiatae*)
xv—Semine nudo polyspermo (*Ranunculus*, *Rosa*, *Alisma*)
xvi—Pomiferae (*Cucurbitaceae*)
xvii—Bacciferae (*Rubus*, *Smilax*, *Bryonia*, *Solanum*, *Menyanthes*)
xviii—Multisiliquae (*Sedum*, *Helleboreae*, *Butomus*, *Asclepias*)
xix—Vasculiferae monopetalae (Various)
xx—Vasculiferae dipetalae (Various)
xxi—Tetrapetalae siliquosae (*Cruciferae*, *Ruta*, *Monotropa*)
xxii—Leguminosae
xxiii—Pentapetalae vasculiferae enangiospermae (Various)

Monocotyledones (singulus aut nullis cotyledonibus)

xxiv—Graminifoliae floriferae vasculo tricapsulari (*Liliaceae*, *Orchideae*, *Zingiberaceae*)
xxv—Staminae (Grasses)
xxvi—Anomalae incertae sedis

B. PLANTAE GEMMIFERAE (ARBORES)

(a) *Monocotyledones*

xxvii—Arbores arundinaceae (Palms, *Dracaena*)

(b) *Dicotyledones*

xxviii—Arbores flore a fructu remoto seu apetalae (*Coniferae* and various others)
xxix—Arbores fructu umbilicato (various)
xxx—Arbores fructu non umbilicato (various)
xxxi—Arbores fructu sicco (various)
xxxii—Arbores siliquosae (woody *Papilionaceae*)
xxxiii—Arbores anomalae (*Ficus*)

Starting with JUNG's definitions and terminology, RAY carefully investigated and extended the entire subject. Having travelled and studied plants in the field under various conditions from Scotland to the Mediterranean, he could appreciate the variability of plants in different habitats. There is evidence that he pondered the species concept more thoroughly than any of his predecessors. He was pretty well convinced that species were constant, although there were certain minor variations in every species. The species character was transmitted from parent to offspring, the minor characters were more indeterminate. He may appear to be a bit inconsistent in giving credence to certain prevalent beliefs that *Triticum* may change into *Lolium,* but there is little evidence that he believed in the mutability of species. When one considers the state of botany as RAY left it and compares it with what JUNG found after the time of the herbals, he is impressed with the advances made in the seventeenth century.

Microscopy and micrography in the seventeenth century:- The first compound microscope was undoubtedly made by ZACHARIAS JANSSEN, a spectacle maker of Middelburg, Holland, who about 1590 presented to CHARLES ALBERT, Archduke of Austria, an instrument which he had made. That primitive microscope was about six feet long, was mounted on a thick ebony board, and contained only two lenses.

ROBERT HOOKE (1635-1703) is credited with being one of the first to apply the microscope to biology and its usefulness was demonstrated by results which he published in Micrographia (1665). HOOKE was an anomalous character, no more biologist than a physicist, technician, philosopher, or chemist, but he devoted himself so industriously to research that there was scarcely a discovery made in his day that he did not hesitate to claim as his own. The Micrographia which contained observations on feathers, lice, fleas, etc. is largely an assemblage of curiosities, but among them is a trenchant observation on the structure of thin sections of charcoal, which he compared with cork and other tissues. He found that the cork was "all perforated and porous, much like a honey comb, but that the pores of it were not regular". He called the pores "cells" and the separating walls "interstitia".

HOOKE became strangely interested in cork and reached the conclusion that it must be the outgrowth of the bark of a tree, and estimated that a cubic inch of cork contained more than twelve hundred million pores. Continuing, he said:

> Nor is this kind of texture peculiar to cork only; for upon examination with my microscope, I have found that the pith of an Elder, or almost any other tree, the inner pulp or pith of the Cany, hollow stalks of several other vegetables — as of Fennel, Carrets, Bar-docks, Teasels, Fearn, some kinds of Reeds etc., have much the same kind of schematisme, as I have lately shown that of cork . . .

It is important to notice that HOOKE conferred the name "cell" on the units of plant structure, and that it has been retained, though used in a sense different from what HOOKE had in mind.

ANTHONI VAN LEEUWENHOEK (1632-1723) cloth merchant and wine-taster by trade, and a correspondent of the Royal Society of London, is another engaging figure in the history of the 17th century. In 1654 he married and settled in Delft, where he lived the remainder of his long life. He devoted his spare time to lens

grinding and making microscopes. It is said that he made over 400 microscopes, of which he bequeathed 26 to the Royal Society of London. Owing to his skill in grinding lenses he developed that art further than anyone had done previously. With his superior microscopes and unwonted powers of observation he made discoveries which became classical. He examined all sorts of things much as HOOKE had done, and with as little attempt to organize them into a definite system. The forms and activities of animalcules in bodies of water, gutters, and ponds were studied and faithfully described. He discovered protozoa and bacteria in the course of his work. Naturally, he did not know what they were but he made drawings of them. He did, however, come to the very definite conclusion that they reproduced their own kind, instead of arising spontaneously. He was the first to observe the striation of muscle fiber and the red blood corpuscles, and was the first to prove that arteries and veins were actually connected by networks of capillaries, and thus completed HARVEY's discovery.

The results of LEEUWENHOEK's work were transmitted in discursive letters to the Royal Society of London. LEEUWENHOEK made no attempt to apply his discovery of microbes to a theory of contagion. He discovered them in waters and infusions, even in the bodies of living animals, but appears never to have suggested in his writings that such "animalcules" threw any light on the etiology of morbid infections. Many years were to pass before the full significance of his discovery was realized.

The inception of plant anatomy:- The science of plant anatomy was founded in the 17th century by two men of outstanding ability, MALPIGHI and GREW, whose results were simultaneously laid before the Royal Society of London in 1671.

MARCELLO MALPIGHI (1628-1694) was born near Bologna and at an early age entered that university where he distinguished himself as a student. He was intermittently a professor in the university until 1691, when his health demanded his retirement, and he went to Rome as private physician to the Pope. With the help of the newly invented microscope, MALPIGHI was intent on discovering all he could about the anatomy and physiology of plants. Although we of this time can see many mistakes in his observations and explanations, they contain much which is still useful. While studying the anatomical structure of stems he was continually concerned with the movement of sap and the translocation of foods, although little was known at the time about the functions of the organs of plants. He was thus interested in building up an integrated knowledge of the plant. Omitting an account of his pertinent discoveries in animal physiology we pass to his work on plant anatomy.

Following a paper presented to the Royal Society he published "Anatome Plantarum" in 1675. This exceptional work dealt with the anatomy of plants and considered their functions. He began with the stem and its bark, which he saw was composed of tiny sacs (utricles), *i.e.*, of cells. In the wood he distinguished fibers, tubes, and other constituents, and he concluded that the wood of trees grew by periodic transformations of the inner bark into wood. The fibers, said he, were for the conduction of water and the tubes for the conduction of air, which is as important for plants

as for animals. The name tracheae which he bestowed on the vessels in stems and on the air tubes in insects is an example of his search for analogies between plants and animals. His belief that there were peristaltic movements in the tracheae lasted long after his time. The important discovery that the layers of tissues in leaves and young shoots are continuous with those of the main stem was made by MALPIGHI. His concept of tissues as exemplified in the following quotation enabled him to clear up many mistakes concerning roots.

> The roots of trees are a part of the stem, which divides into branches and ultimately ends in capillary threads; trees are therefore essentially fine tubes which run separate from one another under the ground, but gradually collect into bundles; these bundles unite further on with other and larger bundles, and all together ultimately join to form a single cylinder, the stem, which then by a separation of the tubes at the opposite extremity stretches out its branches, and by the continued gradual separation of the larger into smaller bundles, finally expands into leaves, and so reaches its furtherest limits.

To MALPIGHI belongs the credit of discovering stomata of leaves and of rightly understanding their function. He compared buds from which leaves and branches arise with the ovary and uterus; leaves were the places in which sap is elaborated, and flowers were described with extraordinary care. He arrived at the curious conclusion that the flower leaves were organs for the excretion of ignoble saps in preparation for the formation of noble fruits. However, he described accurately the seed coat and the process of germination and held fairly correct ideas on the nutrition of plants.

The second part of the "Anatome Plantarum" began with a description of the germination and growth of the seedling, followed by a long chapter on galls which were therein for the first time correctly described. He knew that the galls on legume roots were not produced by insects.

NEHEMIAH GREW (1628-1711) who, jointly with MALPIGHI, founded the science of plant anatomy, was born at Coventry. His education was obtained at Pembroke Hall, Cambridge, and subsequently at Leiden where he received the degree Doctor of Medicine in 1671. Returning to England he practiced medicine at Coventry and subsequently in London. He never held a position in a university, devoting his time to his professional duties and his scientific researches, becoming Secretary of the Royal Society in 1677. He was a man of genius and skill, endowed with the spirit of research. He published "The Anatomy of Plants Begun" in 1672 and "The Anatomy of Plants" in 1682.

GREW saw clearly the problems of plant anatomy and physiology. His drawings are especially commendable, being more exact than those of MALPIGHI. His combined representations of cross and longitudinal sections of stems still can be used for delineating the structure of wood. It is not too much to say that in their time and with their equipment GREW and MALPIGHI advanced the science of plant anatomy as far as was possible. No important advance on their ideas on plant anatomy was made for more than a century.

GREW dealt primarily with the histology of tissues, not with individual cells, nevertheless his casual observations on the union

of cells with each other and on the structure of fibers and vessels formed the basis for the researches of later histologists. We owe to GREW the term "parenchyma". He compared its structure to "the froth of beer or eggs", remarking that the sides of the "bladders" are as transparent as water, or the bodies of some insects. GREW thought that the cells, fibers, and vessels were bound together by a web (partly longitudinal, partly transverse) of finest threads. In this he must have been unwittingly led astray by torn spiral threads in the preparation. He said that the trunk is composed of skin, cortical body, ligneous body, insertions, and pith. He described the structure of the wood more precisely than any predecessor, saying that the lignified part "is nothing else but a cluster of innumerable and most extraordinary small vessels or concave fibers", and found nothing corresponding to valves in the pores or vessels to regulate the flow of sap. He thought that the structure of pith was similar to that of honey comb. The most exact comparison he could conceive of the whole body of the plant was with a piece of fine lace tissue, such as women make on a pillow, for the pith, the medullary rays, and the parenchyma of the cortex "are all extream Fine and Perfect Lace-work".

GREW was not particularly clear about the flower structure because he did not comprehend its nature, nor indeed, did anyone else at that time. He named the parts the "impalement" (calyx), the "foliation" (corolla), and the "attire".

The ideas of MALPIGHI and GREW on leaves are worth reproducing since they were so pertinent and each in his way marked an advance. The following excerpts are shown in parallel columns.

MALPIGHI - *The leaf.*

In their development Nature is so fertile that plants appear to vegetate on account of the leaves. The leaves are arranged in different positions and order on the shoots and outgrowing buds; frequently in trees they break forth in alternating order, as we see in *Populus, Laurus, Corylus, Citrus, Rosa canina, Castanea vesca, Rhamnus, Jujuba.* On these 23 or more leaves may sometimes grow from one twig, and those in the middle of the twig are larger and wider, the others smaller.

Moreover the alternately placed leaves take no definite position so that two straight lines drawn from base to apex would not touch all the leaves, on the contrary they are placed in different order, so that every third leaf points in the same direction. However, in others like the oak from whose lengthy shoots numerous leaves arise it is difficult to discover a symetry.

GREW - *On leaves.*

Another use (of leaves) is for augmentation; or the capacity for the due spreading and ampliation of a Tree or other Plant, are its leaves. For herein the Lignous Body being divided into small Fibers, and these running all along their lax and spongie Parenchyma; they are thus a body fit for the imbibition of sap and easie growth. Now the Sap having a free reception into the leaves, it still gives way to the next succeeding in the Branches and Trunk, and the voyding of the sap in these, for the mounting of that in the Root, and ingress of that in the ground. But were there no leaves to make a free reception of sap, it must needs be stagnant in all the parts to the Root, and so the Root being clogg'd its fermenting and other offices will be voyded and so the due growth of the whole. As in the motion of a Watch, although the original term thereof be the Spring, yet the capacity for its continuance in a due measure throughout all the wheels, is the free and easy motion of the Ballance.

It is appropriate to comment on the relations between these two eminent men, lest there be any misconceptions on the subject. GREW's innate modesty and professional appreciation of MALPIGHI's work impelled him at one time to cease his researches and leave the field to his Italian rival, but the Royal Society urged him to continue them and in 1672 appointed him curator to the society for the anatomy of plants. GREW was deeply conscious of this honor expressing nothing but praise for MALPIGHI and his work. MALPIGHI exhibited an equally courteous spirit and had GREW's

work translated into Latin for his own use. We cannot but admire this example of scientific courtesy.

Physiology in the seventeenth century:- In this epoch when the subject of plant physiology was begun, men's attention was directed to the physics of absorption and translocation of sap. Their minds were undoubtedly turned in that direction by HARVEY's discovery of the circulation of the blood. "This discovery of HARVEY's created an immense sensation; during the immediately succeeding decades after its publication (in 1628) it was the one great question of the day and occasioned a vast quantity of literature both for and against it" (NORDENSKIÖLD, p. 141).

JUNG's views on the absorption of substances by roots have already been mentioned. He seemed to have had some idea that roots exercised a selective power in absorbing substances, but it was crudely stated. The fruitful investigations of MALPIGHI and GREW afforded a sound basis for their discussions of the problems of sap translocation in plants. Their attempts should be emphasized in view of the fact that no advance in this field had been made for nearly 2000 years.

MALPIGHI said "There are several kinds of vessels in plants both in the bark and in the wood in addition to latex tubes and resin canals; the sap can flow upwards and downwards as we see when a branch continues to grow after having been bent downwards. Furthermore, if a part of a leaf be cut the sap can make new paths". He believed that the sap absorbed by roots ascended through fibrous constituents of the wood and that air ascended through tubes he named tracheae on account of their resemblance to the breathing apparatus of insects. MALPIGHI broke from teleological moorings. He proceeded to formulate a general theory of sap circulation based upon patient, thorough-going observations including the function of the leaves. In all this he rested on the secure foundation of his discovery of the continuity of tissues throughout the plant.

GREW's ideas on sap movement in plants were hardly as successful as MALPIGHI's. We can credit him, however, with the idea that the sap ascends solely through the wood and with recognition of the role of capillarity aided by lateral pressure of the turgid parenchyma. He thought that the rise in the wood occurred only in the spring, that for most of the year it rose in bark. He seems to have had no adequate conception of the role of a living substance which constituted a definite part of the organism, but he was secure in his knowledge of the continuity of the vessels in wood, leaf, etc. He refers many vital phenomena to "fermentation", a term endowed with mystery in his day as well as in ours.

It would be futile to put into the statements of MALPIGHI and GREW meanings which obviously had not dawned at that time. They should be extolled, however, for their work on plant anatomy with its emphasis on physiology. Had they lived and worked two centuries later, they would most certainly have given a splendid exposition of the movement of sap and of its physiological functions. Both men repeatedly emphasized the importance of leaves as organs for the elaboration of food.

J. B. VAN HELMONT (1577-1644) was one of the greatest chemists who preceded LAVOISIER. He devoted much attention to the

study of gases, and is supposed to have been the first to use the word gas as a generic name for all elastic aëriform fluids. He was also the first to take the melting point of ice and the boiling point of water as standards of the measurement of temperature. The process of fermentation, he said, must produce a kind of air similar to that which is liberated when charcoal is burned, or which sometimes renders the air of caves unfit for respiration.

VAN HELMONT performed an experiment on plant growth in which crude quantitative methods were used, and although he was erroneous in his conclusions and his work received no immediate scientific attention, he did something to combat the Aristotelian idea of plant nutrition. The oft-quoted experiment was as follows:— He planted a willow branch weighing five pounds in a pot containing 300 pounds of dry soil. The pot was given nothing but water. A cover prevented solid matter like dust from falling on the surface of the soil. When the experiment was discontinued at the end of five years, the willow had grown to a tree weighing 164 pounds, and the soil weighed only two ounces less than at the beginning. VAN HELMONT concluded from this result that the increased mass of the tree had been derived from the water and not from the soil, and that the tree made all of its substance from the water absorbed. VAN HELMONT was more than two centuries ahead of his time, and may therefore be pardoned for his conclusion. He deserves credit, however, for experimenting on the question and for drawing conclusions which rested on the results obtained and not on the classical ideas of plant nutrition. At last there was an idea that the nutriment of plants is not obtained like that of animals.

EDME MARIOTTE (c. 1620-1684), who was active in developing experimental research in France, incidentally paid some attention to the physiology of plants. He opposed the prevalent Aristotelian theory of plant nutrition and attempted to substitute for it the concept that the whole process of plant life and nutrition is based upon physical forces. He did not experiment on plants, but made some very pertinent observations, stating that *e.g.*, if one grafts a scion of "Bon Chrétien" pear on a wild root, the sap of the latter nourishes both the graft and the stock. On the former it produces well-flavored fruits; on the latter only wild fruit, conversely, if one grafts a scion of the wild on the cultivated pear, the tree thus grafted produces only wild fruits. The sap of the original (stock) trunk therefore acquires different qualities in each graft, as shown by the character of the fruits. Another nail in the coffin of the classical theory of nutrition was driven by the observation that diverse species of plants find, in the same soil, substances necessary for synthesizing a great variety of materials.

MARIOTTE's interests in physical science led him to think about the flow of sap in plants. The ascent of sap was ascribed to capillarity, but he thought that the latex corresponded to the arterial blood, and the watery sap to the venous blood.

Botanical explorers and explorations:- HANS SLOANE (1660-1753) a man of talent, education, and personality studied in London, Paris and Montpellier. At the age of 28 he embarked for the West Indies as physician to the Duke of Albemarle, eventually arriving in Jamaica.

"He was", says PULTENEY, "the first man of learning, whom the love of science alone had led from England, to the distant parts of the globe; and, consequently, the field was wholly open to him. He was already well acquainted with the discoveries of the age. He had an enthusiasm for his object, and was at an age, when both activity of body, and vivacity of mind, concur to vanquish difficulties".

Dr. SLOANE returned from his visit to the West Indies in May 1689 bringing a collection of not fewer than 800 species of plants, a number much larger than anyone had hitherto brought to England. He published an account of Jamaica plants in his Catalogus plantarum (1696) following, as far as possible, RAY's system, and eliminating synonymous names. RAY eventually incorporated SLOANE's list of plants in the third volume of his Historia plantarum generalis. In addition to his activities in establishing the Chelsea botanical garden and to his duties as president of the Royal Society of London, SLOANE found time to describe plants, correspond with JOHN RAY, and to form a scientific collection and library which, after his death, formed the nucleus of the British Museum. The figure of this eminent man is still conspicuous after two centuries.

JAMES CUNNINGHAM, who investigated the flora of China more thoroughly than any European had formerly done, was sent in 1698 to China as physician to the English factory at Amoy. CUNNINGHAM appears to be the first English writer who gave an accurate description of the tea tree, and has the distinction of being the first European who made botanical collections in China and whose rich herbarium safely arrived home. He sent to PLUKENET and PETIVER a large number of new plants which they studied and described.

While European botanists were collecting and accurately describing their flora, an epoch-making piece of work was being done by RUMPHIUS (GEORG EBERHARD RUMPF) (1628-1702) in the Moluccas. Having been appointed to a post by the Dutch East India Company, he went out in 1653 and took up residence on the small island of Amboina southwest of Ceram which was important to his employers on account of its spices. RUMPHIUS' assiduous work on the natural history of Amboina and adjacent islands won for him the appropriate name, "the Pliny of the Indies". His work made the world better acquainted with this small out-of-the-way island than with many a larger and more frequented area.

MERRILL wrote (1917), "The flora of Amboina is typically Malayan, although a few Australian types are present as in other parts of the Malayan region. Practically all of the species found along the sea coast are of general distribution from India to Malaya and Polynesia. Likewise most of the species found in the settled areas at low and medium altitudes, weeds of cultivation, and the generally cultivated economic and ornamental plants are the same as those usually found throughout Malaya, very many of which are now distributed in all tropical regions. . . . From the standpoint of endemic species most of the neighboring islands are probably of much greater interest than is Amboina, but from the standpoint of the history of Malayan botany, no part of the Moluccas can be compared with it".

RUMPHIUS' renowned work, the "Herbarium Amboinense" (1741-1755), contains descriptions and illustrations of the flora of that island which are truly remarkable when one realizes that all was the work of one man who labored under tremendous handicaps. He described and named about 1700 forms. Many of RUMPHIUS'

forms were certainly varieties. His idea of species was naturally not that which is held today, yet his pioneer work has an abiding value. Although the work was pre-Linnean and exemplifies no definite system of classification, subsequent writers made the Rumphian descriptions (and figures) the types of many binomials. LINNAEUS made reference to very few Rumphian names in the first edition of Species plantarum, but his successors adopted many of them. LINNAEUS based certain binomials on the illustrations and descriptions in RUMPHIUS' "Herbarium" but wrote no descriptions other than those he took from RUMPHIUS. LINNAEUS and his pupil, STICKMAN, attempted to reduce the "Herbarium" to the binomial system (1754), but no botanical specimens from Amboina were available to European botanists until late in the 18th century and then the numbers were small.

The tragic circumstances under which RUMPHIUS' work was done must not be overlooked. From his arrival on Amboina in 1653 he worked assiduously on the Herbarium and in 1670 had nearly finished, but was anxious (as many another botanist has been) to make one more trip of observation. This last trip, he admitted, was responsible for the blindness which afflicted him the rest of his days. Nevertheless, with the help of his wife and of men sent by the Dutch East India Company he worked on. He was engaged in a translation of the Latin text of his work into Dutch when in 1674 the island experienced a great earthquake in which his loyal wife and eldest child were killed. He continued the work with such help as he could get, but in 1687 suffered the loss of some of his precious manuscripts and the illustrations for the Herbarium by a fire which also destroyed his house and his library. Yet his courage was not daunted, with almost incredible devotion he renewed his work and replaced all the lost illustrations, utilizing the talents of his son and such other assistance as he could get.

The manuscripts of the first six books were eventually finished in 1690 and sent to Batavia, Java, to be transmitted to Europe. But apparently ill-fortune followed them, for the ship "Waterland" on which they were carried was destroyed by the French and the precious manuscript was lost. A copy of the manuscript had been kept, however, from which the work was reconstructed, but it was some years later before a new copy was sent to Holland. The manuscript of the Auctuarium which RUMPHIUS completed only a few months before his death was copied at Batavia and sent to Holland two years after the death of RUMPHIUS at Amboina. The Herbarium Amboinense laid in the offices of the Dutch East India Company for over 30 years before it was edited and published.

The light kindled by this valiant man has illumined the scientific studies of the Indo-Malayan flora for over two centuries, thanks to his spirit which knew no defeat.

REFERENCES:

DOBELL, C. (1932): Antony van Leeuwenhoek and his "Little animals". Harcourt, Brace, New York.

GREEN, J. R. (1914): A history of botany in the United Kingdom. Dent & Sons, London and Toronto; Dutton, New York.

Haarlem, Koloniaal Museum (1902): RUMPHIUS Gedenkboek, 1702-1902. J. H. de Bussy, Amsterdam.
HAWKS, E. (1928): Pioneers of plant study. Sheldon Press, London; Macmillan, New York and Toronto.
MERRILL, E. D. (1917): An interpretation of RUMPHIUS' Herbarium amboinense. Bureau of Printing, Manila.
NORDENSKIÖLD, E. (1928): The history of biology (transl. from the Swedish by L. B. EYRE). Knopf, New York and London.
PULTENEY, R. (1790): Historical and biographical sketches of the progress of botany in England. Cadell, London.
SACHS, J. VON (1890): History of botany (1530-1860) . . . authorized transl. by H. E. F. GARNSEY . . . rev. by I. B. BALFOUR. Clarendon Press, Oxford. (Original German ed., 1875).
SCHMUCKER, T. (1936): Geschichte der Biologie. Vandenhoeck & Ruprecht, Göttingen.

Chapter VII.

THE EIGHTEENTH CENTURY.

The remarkable gains of the 17th century were the vehicles of scientific thought for many a day. The freedom to investigate things in the universe and the invention of lenses pushed forward the biological sciences. If science was less inventive in the 18th century, it, nevertheless, had the merit of solving some of the problems inherited from by-gone ages. Happily, so far as the plant sciences were concerned, the mystifying attitude of the ancients had been dispelled and the age of the experimentalist was at hand.

Discovery of sexuality in plants:- The nature philosophy of the Greeks had contributed nothing of value to the proper understanding of the process of fertilization in plants. The empirically derived knowledge of the Assyrians and Chaldeans concerning the necessity for pollinating the pistillate spathes of the date-palm was repeated by THEOPHRASTUS and PLINY. It is possible that PLINY understood that the process of fertilization required the transfer of a *material* from one to the other, and that this material was the pollen dust. CESALPINO reiterated the Aristotelian doctrine that the production of seeds was simply a nobler form of reproduction than that by buds. MALPIGHI was silent on the subject, and GREW got only far enough to say, "That the same plant is both male and female, may the rather be believed, in that snails and some other animals are such" (Anatomy of Plants, 1682). As early as 1686 RAY had admitted that the existence of sexuality in plants was probable but that it required more proof. It is all too evident that the question of sexuality baffled those who used only observational and descriptive methods. The answer was obtained by those who used experimental methods — the new tool of biological research.

Although the epoch-making discovery of RUDOLPH CAMERARIUS (1665-1721) was published in the closing years of the 17th, we shall include it in a survey of the 18th century. He became Professor Extraordinary and director of the botanical garden at Tübingen in 1688, and professor of physics in 1689. He was a botanist of renown who reported his results in letters to savants in other universities.

A female mulberry tree observed by CAMERARIUS once bore fruit although no male tree was in the vicinity, but the berries were seedless. This led him to extend his investigation by separating dioecious plants in a garden. He set two female specimens of *Mercurialis annua* apart from others and watched their seed formation. The plants grew well but were seedless in contrast to others which were amongst male plants. On August 25, 1694 he wrote a letter entitled "De sexu plantarum epistola" to VALENTIN, a professor at Giessen, in which he painstakingly discussed

the views of ancient writers on the flower and concluded with an account of his own results. He reported that when he removed the male flowers of *Ricinus* and *Zea mays* he got no seeds. From this he concluded that no ovules of plants could ever develop into seeds without first being prepared by the pollen which is borne in the stamens. "It therefore follows", said he, "that the stamens are the male sexual organs in which that powder which is the most subtle part of the plant, is secreted and collected, to afterwards be supplied from thence". In these words the process of fertilization was more correctly explained than ever before. The whole tone of the letter shows that CAMERARIUS was deeply impressed with the extraordinary importance of the question, and that he was concerned to establish the existence of sexuality on a secure basis. Probably his most important statement was that in which he came to the conclusion that the "apices" with their pollen are the male; and the style and ovary are the female organs in the flower.

Among CAMERARIUS' many experiments were several failures, which, in his scientific way, he took pains to report. He was much disturbed to find that three plants of hemp taken from the field and set in the garden produced fertile seeds, and upon repeating the experiment by growing the plants indoors in pots, he obtained the same results. In this case it seems that he left to someone else the cutting out of the male plants.

The importance of CAMERARIUS' discoveries soon became appreciated by other investigators; some denied them; others declared they knew them all the time; but here and there, some were sufficiently aroused to put them to the test. Among the latter was JAMES LOGAN (1674-1751), governor of Pennsylvania. He set some plants of corn at opposite ends of a plot of ground, about 80 feet apart. In one group he left the plants intact, but from the others he removed the male panicles. Late in the summer he observed that the ears of the hills in which the plants had been decapitated were all sterile except "one large ear which grew out somewhat further from the stalk than usual, and on that side too, which faced another hillock in a quarter from which our strongest winds most commonly blew". An ear among the unmutilated group, which had been wrapped in muslin, remained without a fertile seed. It thus appears that LOGAN may be credited with the first appreciation of wind pollination. The exact date of this work is not known, but it appears to have been published in 1739.

Years passed before anything more of importance was done. J. G. GLEDITSCH (1714-1786), director of the botanic garden in Berlin, endeavored to attain perfect conviction on the point by many years' experiments with diverse plants. A female palm (*Chamaerops humilis*) which had been brought to Berlin from Africa had never been known to produce seed, though it was about eighty years old, and he himself had observed it for about fifteen years. There was no male tree in Berlin, so he procured part of a male inflorescence from a tree growing in Leipzig, from which he obtained pollen, dusting it over the female flowers and tying it on to the inflorescence of the Berlin tree. The result was that fruit ripened the following winter and germinated in the spring. Though this was only doing once more what HERODO-

TUS had reported the Assyrians as doing in the fifth century B.C., it was experimental proof of the sexuality of plants.

Attempts to discover the facts about reproduction in plants were thereafter made by VAILLANT, LINNAEUS, and others, but the next definite advance in this field was made by J. G. KOELREUTER (1733-1806) who conducted his experiments partly in the town of Calw in Wurtemberg, and partly in St. Petersburg, Berlin, and Leipzig. From 1764 to his death in 1806 he was professor of Natural History in Karlsruhe. He discovered the function of nectar and the role of insects and wind in the pollination of flowers, and, most important of all, he made plant hybrids. He wrote graphically and with poetic grace. His first and most important work entitled "Vorläufige Nachricht von einigen das Geschlecht der Pflanzen betreffenden Versuchen" was published in four parts in 1761, 1763, 1764 and 1766.

KOELREUTER described for the first time the process of natural pollination in *Iris, Malva,* and other plants, concluding that flowers that were incapable of pollinating themselves were pollinated by insects. In order to discover how effective insects were in the fertilization of flowers, he pollinated 310 with a brush, leaving the same number to be pollinated by insects. The number of seeds formed in the latter case was only a little less than in the former. Having interested himself thus far in pollen, he proceeded with the microscope available in his day to study the structure of the pollen grain and successfully described the double wall with its exterior sculpturing. He noticed that something escaped from the pollen grain after it had lain for some time on the stigma and fancied that this something was an oil, which united with another oil secreted by the stigma, and that the combined fluids passed down the style to the ovary and there induced the formation of the embryo.

GLEICHEN and others had thought that pollen grains contained spermatozoa and must burst to discharge them in order to effect fertilization, but KOELREUTER did not regard the bursting of the grains as a natural process, since they obviously possessed devices for its prevention. He started with the hypothesis that the oil on the surface combined with the moisture of the stigma forming a new substance, as an acid and an alkali unite to form a salt, and that this substance, if fertilization is to ensue, must be absorbed by the stigma and conveyed through the style to the ovules. This view he later retracted, finding it to be inconsistent with the facts revealed by his experiments in hybridization.

KOELREUTER's fame rests upon his hybrids between *Nicotiana paniculata* and *N. rustica* and his discovery that the hybrids were sterile. He made other crosses between species of *Dianthus, Hyoscyamus, Ketmia, Matthiola,* and *Verbascum* and learned that hybridization is, in general, only possible between nearly related plants. By pollinating the stigmas with pollen taken from another species, he established the prepotency of pollen taken from other flowers of the same species, and concluded that in the natural state of things and under ordinary conditions hybrid plants are with difficulty produced in nature.

We pass to one of the most engaging botanists of the 18th century. CHRISTIAN KONRAD SPRENGEL (1750-1816), author of an interesting book entitled "Das entdeckte Geheimniss der Natur

im Bau und in der Befruchtung der Blumen". Published in 1793, one hundred years after the publication of CAMERARIUS' "De sexu plantarum epistola", it contained the results of brilliant researches. The purpose of the book was the explanation of the structure of flowers, their colors and odors. It exhibits much of the spirit and method of DARWIN but is often stifled in a teleological atmosphere.

While employed as pastor of the church at Spandau, SPRENGEL became interested in the study of botany and as his interest in botany grew, he neglected the duties of his office, the Sunday sermon being often entirely omitted. Finally he lost his church and went to Berlin where he lived in straitened circumstances, shunned by men of science on account of his eccentricities. There he supported himself by giving instruction in languages and botany, using his Sundays for excursions which anyone might join on payment of a fee of a few groschen. Inevitable disgust with the way in which his work was treated led him to forsake botany and devote himself to languages.

In "Das entdeckte Geheimniss" SPRENGEL examined the common wild flowers of his country, noting the adaptations they show to their environment and to insects. Setting out with the conception of a "Wise Author of nature who has not created one hair without a definite purpose", SPRENGEL's study of apparently insignificant facts brought about much clearer understanding of the meaning of flowers than had ever been given before. He first regarded the modifications of the flower as existing for the sole benefit of insects, but later the study of some species of *Iris* led him to the conclusion that the whole structure of the flower was an adaptation to secure pollination by one or several species of insects. SPRENGEL showed cross pollination to be the rule rather than the exception and stated that, "Since very many flowers are dioecious, and probably at least as many hermaphroditic flowers are dichogamous, Nature appears not to have intended that any flower should be fertilized by its own pollen". Dichogamy, the maturing of stamens and pistils at different times, had been previously noted by KOELREUTER but without appreciation of its significance.

SPRENGEL noted that the markings of petals and their colors could serve to guide the insects to the nectar glands. He distinguished between anemophily and entomophily. He showed that all flowers "which are without a proper corolla and have no calyx in its place, are destitute of nectar and are not fertilized by insects, but by some mechanical means, as by the wind". He also observed that such flowers produced light pollen and in large amounts, while the reverse was true of insect-pollinated flowers. He indicated that all the devices of flowers, whether for insect pollination or for wind pollination, pointed indubitably to the fact that as far as possible, nature avoided self-pollination. Thus we have the problem of cross pollination stated. It rested here for a long time. CHARLES DARWIN was the next to study it and to answer the question why it should be so.

Studies on Fungi:- In the 18th century botanists began to give some attention to the nature of fungi. As early as 1729 PIER'-ANTONIO MICHELI (1679-1737) had observed that germinating

spores gave rise to threads and that these ultimately produced sporophores.

"Methodus Fungorum" (1753) is a small work, illustrated with six good plates, in which the author, J. G. GLEDITSCH, classified fungi into 11 genera, such as *Byssus, Clavaria, Agaricus, Peziza,* etc.

MATHIEU TILLET (1714-1791) made protracted observations on the cause of wheat smut (bunt) and published his dissertation in 1755. Although he failed to discover the causal fungus, he established the fact that the disease was transmitted by the smut dust on the seed. FELICE FONTANA (1730-1805) in 1767 gave a clear account of the nature of grain rust which he ascribed to a fungus parasitic on the plant. He found hyphae but was disappointed because he could not find the "flowers, seeds, or buds".

A reversion to the assumption that all diseases of plants were non-parasitic is seen in the dissertation by J. C. FABRICIUS (1745-1808) published in 1774 and in ZALLINGER's "Morbis Plantarum" (1779) which holds that fungi are the product rather than the cause of disease.

Progress in plant classification:- By the middle of the 17th century the number of plants known and named had become so large that chaos resulted from all attempts to classify them by any system then known. All who worked persistently on the problem felt the need of a more orderly system. THEOPHRASTUS and others had made a crude classification of plants into trees, shrubs, and herbs, utilizing very obvious characters. In the course of time, however, it became apparent that classification must be based on characters of greater fundamental importance than either relative size or longevity.

KASPAR BAUHIN, who distinguished genera and species by names and frequently used a binary nomenclature, had made a great advance on FUCHS. CESALPINO had suggested a definite and logical arrangement into classes based on the characters of the seed and embryo, but his work had little influence either upon his contemporaries or his successors. RAY, who distinguished monocotyledons and dicotyledons, has already been discussed.

Without mentioning several others whose contributions served to clarify the problem of classification, we may next consider CAROLUS LINNAEUS (1707-1778), who profoundly impressed himself and his work on botany in his own and succeeding generations. LINNAEUS elaborated a skillful system of plant classification called the "sexual system" because it employed the stamens and pistils as critical characters.

In view of the numerous biographies of LINNAEUS, the following brief sketch of his life will suffice. His birthplace was Råshult, in the province of Småland, Sweden. Dissatisfied with the University of Lund, where he started his educational career, he went to Upsala, where he came under the influence of CELSIUS. Seeking to widen his knowledge by travel and field work, he made an excursion to Lapland which appears to have left a permanent impression on the man. On later journeys to Holland, France, and England, he met prominent naturalists of the time. Refusing offered positions, he returned to Sweden and was, in 1741, appointed to the coveted position of professor of botany at Upsala in which he

remained until his death in 1778. The admiration and esteem he won are attested by the many honors he received, and by the great number of earnest students who sought him out in Upsala. He trained an enthusiastic group of naturalists and sent out collectors to discover new plants which would fill up the gaps in the system of classification. Throughout his life he retained an engaging naïveté, tinged often with romanticism. He referred all causes to the Eternal Being whom he regarded as the first great Cause, and he believed that species were immutable.

Of his numerous writings we can mention only a few — Systema Naturae (1735), Genera Plantarum (1737), Philosophia Botanica (1751), and Species Plantarum (1753).

Although LINNAEUS showed no genius for original scientific work such as JUNG's, he had a great mind and has made succeeding generations his debtors for his powers of analysis, description, and diagnosis. His system of classification, in spite of its short-comings, was workable and was adopted by botanists in Germany and England, as well as in Sweden. It was left for others to establish systems in which natural relationships were more accurately recognized.

LINNAEUS' system was obviously simple; for example, plants whose flowers contained one stamen were in the class Monandria, those with two stamens, in Diandria, and so, Triandria, Tetrandria, Pentandria, etc. All plants, according to LINNAEUS' system were thus arranged into 24 classes. Arbitrary as it was, it met the needs of the day and was generally welcomed by systematists who were becoming overburdened by the ever-mounting numbers of plants. This system was published in tabular form in the first edition of "Systema Naturae" (1735) and in 1737 in "Genera Plantarum eorumque characteres naturales secundum numerum . . ." (Fig. 31).

The limitations of the system are such as naturally follow when one depends on characters derived from one set of organs instead of considering the aggregate of characters. LINNAEUS had a poor idea of cryptogams, all of which he put into a single class. He also neglected the anatomy and physiology of plants. LINNAEUS himself regarded the "sexual system" as temporary, useful until the affinities of genera could be determined and natural groups established. If he conceived that the construction of a natural system was one of the primary tasks of botany, he was nevertheless far from regarding a "natural" as a phylogenetic system, based on the idea of descent. LINNAEUS firmly believed in the constancy of species, even if in the later course of his life he modified it by subscribing to the new formation of species. In this respect he was more of a medieval than a modern botanist.

LINNAEUS' significance lay not entirely in the creation of his system, but also in the creation of a new and precise nomenclature of botany. The world owes him much for the establishment of the binary system of nomenclature, by which every plant name is expressed by two words — genus and species. Many plants had been known for a long time by binomial terminology (KASPAR BAUHIN and JOHN RAY), but the names were often expanded into three or more terms; *e.g.*, *Gramen geniculatum aquaticum.* LINNAEUS established the rule that every plant should have only two names. By his extensive studies and writings he showed how

this could be done. His concept of the worth of genera and species was perhaps the most important contribution he made to systematic botany. Botanical nomenclature is regarded as beginning with the general application of binomial names to plants in the "Species Plantarum" (1753).

The use of Linnaeus' system was so obvious and convenient that the discovery and classification of plants was in danger of becoming a mere pastime for those who enjoyed cataloguing and sorting plants. Although he did not live to work out a natural system, he supplied certain fundamental ideas upon which others built. His arrangement of genera into orders was based, not on any one distinguishable character, but, as Linnaeus himself said, on the simple symmetry of all parts. In fulfillment of this plan he arranged the genera which he had established into 67 orders and published them in 1751 in the "Philosophia botanica". Strangely enough, he gave no indication of the characters by which they were distinguished. Some of his orders represent natural groups, but since the majority contained inconsistent mixtures, the matter was left by Linnaeus in an extremely unsatisfactory state.

In his own time there was a rising tide of opposition to Linnaeus' system of classification. In Germany opposition came from the followers of Rivinus, founder of a classification based on the divisions and shape of the corolla; Haller, who was hostile to Linnaeus' innovations, also made attempts to substitute other systems. Linnaeus' system was not well received in France. Michel Adanson had again directed the attention of botanists to the existence of natural affinities of plants, and Bernard de Jussieu founded upon them a natural method which is often designated as the system of Trianon, because plants in the Royal Garden were arranged according to it.

Bernard de Jussieu (1699-1777) was a member of a family which through almost a century and a half occupied prominent positions in the Académie des Sciences, in the Royal Gardens, and in the Museum of Natural History in Paris. His brothers Antoine and Joseph were also botanists of merit. The former was successful in the field of economic botany, the latter travelled in the Americas and enriched the Museum with many new plants. Bernard was professor of botany and demonstrator at the Royal Garden.

The de Jussieu genealogy:-

Pierre
|
Laurent
|
Christophe — Antoine — Bernard — Joseph

Christophe
|
Antoine-Laurent
|
Amélie — Adrian

It appears that Linnaeus was immensely impressed by the knowledge of the talented Bernard, who started to arrange the plants in the Royal Garden according to the Linnean system. As he elaborated the plan, he introduced various changes and eventu-

ally the system of LINNAEUS became the system of DE JUSSIEU. Being dissatisfied with its incompleteness, he never published his entire arrangement, but his nephew, ANTOINE-LAURENT DE JUSSIEU (1748-1836) later incorporated it with his own work and published it in "Genera plantarum secundum ordines naturales disposita" (1789).

The system is generally acknowledged to be a triumph in classification according to natural affinities and for the assignment of characters to the smaller groups which we would now call families, but which he called orders. According to A. L. DE JUSSIEU's system there were 100 orders (or families), each carefully characterized. The excellence of his work is attested by the fact that nearly all are still recognized. Let it be noted, moreover, that he was a believer in the constancy of species.

Since this system of DE JUSSIEU was so fundamental for all subsequent progress in the elaboration of natural systems, it is necessary to give a view of it in the following table.

				Class
Acotyledones				I.
Monocotyledones		Stamina hypogyna		II.
		" perigyna		III.
		" epigyna		IV.
Dicotyledones	Apetalae	Stamina epigyna		V.
		" perigyna		VI.
		" hypogyna		VII.
	Monopetalae	Corolla hypogyna		VIII.
		" perigyna		IX.
		" epigyna	antheris connatis	X.
			—— distinctis	XI.
	Polypetalae	Stamina epigyna		XII.
		" hypogyna		XIII.
		" perigyna		XIV.
	Diclines irregulares			XV.

As an illustration we may mention the contents of some of these classes. Class I contained fungi, algae, hepatics, mosses and ferns, and also Naiades, which includes a number of aquatic flowering plants remotely related to the others. Since the exact knowledge of cryptogams had to wait on the development of the compound microscope, it is not surprising that imperfections in classification were included. However, it was an improvement on any preceding system in that respect.

Class II contained the orders *Aroideae, Typhae, Cyperoideae,* and *Gramineae.*

Class III contained the orders *Palmae, Asparagi, Junci, Lilia, Bromeliae, Asphodeli, Narcissi, Irides.*

Class IV contained the orders *Musae, Cannae, Orchides, Hydrocharides.*

Class V contained *Aristolochiae.*

Class VI contained *Eleagni, Thymeleae, Proteae, Lauri, Polygoneae, Atriplices,* and so forth.

It is evident that DE JUSSIEU retained RAY's distinction of Monocotyledons and Dicotyledons although he considered that the Cryptogams were a class of equal rank with them.

The 18th century, therefore, witnessed important fundamental work in plant classification. When the century ended there was established a binary system of nomenclature, based on the genus and species, an exact method of plant description, and a system of classification which was essentially based on natural affinities. The accomplishments in this field of botany in the 18th century outweigh all that had been done in the preceding ages.

Experimental work in plant physiology:- The first physiological work which had a lasting influence was done in the 18th century. The fragmentary work of VAN HELMONT and MARIOTTE stood by itself, stimulating no subsequent work of a similar nature. MALPIGHI was much nearer the truth than any one had been before him when he discovered that plants, as well as animals, require air to breathe and when he repeatedly emphasized the importance of leaves in the elaboration of plant food. His statements have been reported in chapter 6. MALPIGHI was one of the first to consider the physiology of the plant objectively and to coördinate physiology with anatomical organization.

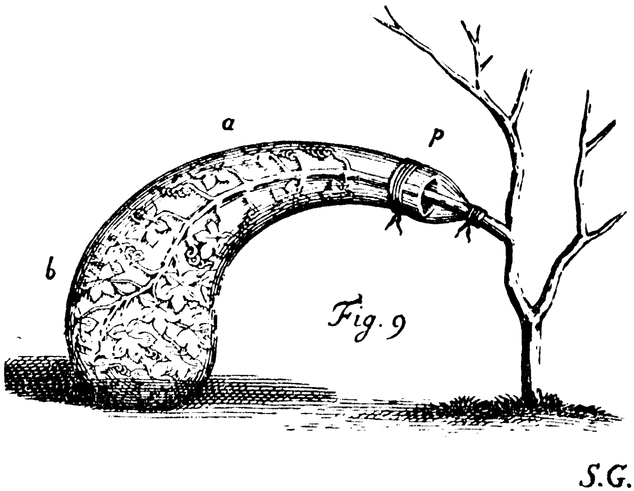


FIG. 16. — HALES' demonstration of a method for collecting the water transpired by plants. From Vegetable Staticks, p. 50 (1727).

STEPHEN HALES (1677-1761) was the first great figure in plant physiology, since he was the first to conduct experiments on plants and to get quantitative results. Some of his experiments, such as those concerned with the movement of sap, are still after the lapse of two centuries, quoted in modern botanical text books. This is in itself, an indication that HALES was a genius of an entirely different order from those who had preceded him in the field of physiology. The circumstances of his life were conducive to study and research. Prominent in the scientific life of his time, honored by universities, active in civic work, an inventor, and perpetual curate of Teddington in Middlesex, he lived a rich and satisfying life. His acquaintance with the works of HARVEY and BORELLI on the mechanics of the circulation of the blood in animals prompted HALES to extend their discoveries with the aid of the new and exact physics which had been elaborated since HARVEY wrote his book. The outcome of that work was Haemostaticks (1733), published as the second volume of his Statical Essays.

The botanical work for which HALES is justly famous is "Vegetable Staticks" (1727) which later formed the first volume of his Statical essays. This work deals with the movements of sap in plants and reflects the influences of NEWTON and BOYLE on HALES. The study of transpiration for which he is so renowned forms the subject of the first part of the book. HALES determined the loss in weight of a potted sunflower plant and measured the leaf and root area with meticulous care. He then repeated the determinations on a variety of other plants. He measured also the cross-section of the main stem of the plant from which he proceeded to calculate the actual velocity of the flow of sap in the plant as he had determined the velocity of the blood stream in animals. He soon discovered that the rate of sap flow varied in different plants. He demonstrated the lifting power of transpiration by recording the passage of water through an apple branch whose base was immersed in water and with genuine critical insight compared it with the amount passed through the adjoining piece of stem under a hydrostatic head of seven feet. These cautious comparisons which he made were unknown before his time.

To clinch the matter of transpired water, HALES went further. His own words may be appropriately quoted:

> Having by many evident proofs in the foregoing experiments seen the great quantities of liquor that were imbibed and perspired by trees, I was desirous to try if I could get any of this perspiring matter; and in order to it; I took several glass chymical retorts, *bap*, (Fig. 9) and put the boughs of several sorts of trees, as they were growing with their leaves on, into the retorts, stoping up the mouth *p* of the retorts with bladder. By this means I got several ounces of the perspiring matter of Vines, Fig-trees, Apple-trees, Cherry-trees, Apricot and Peach-trees; Rue, Horse-radish, Rheubarb, Parsnip, and Cabbage leaves; the liquor of all of them was very clear, nor could I discover any different taste in the several liquors: But if the retort stand exposed to the hot sun, the liquor will taste of the coddled leaves. (p. 103).

It is interesting to see that HALES used the three methods of estimating transpiration which have been employed in modern times, *viz.*, weighing, using a rough sort of potometer, and collecting the condensed moisture.

After the experiments on transpiration, he turned his attention to capillarity and root pressure as factors in raising the sap. HALES was the first to measure root pressure, although the bleeding of trees at certain seasons of the year must have been long known. Patiently repeating the measurements of root pressure, he found that there came a time when the sap did not rise in the manometers. After reporting all of his results, he concluded, "It seems evident, therefore, that the capillary sap vessels, out of the bleeding season, have little power to protrude sap in any plenty beyond their orifices; but as any sap is evaporated off, they can by their strong attraction supply the great quantities of sap drawn off by perspiration". We appreciate the soundness of his reasoning all the more since we realize that the mechanism of root pressure is not yet fully explained. HALES had proof that the sap in plants circulates, not as in animals, but in response to imbibition and transpiration affected by seasonal conditions.

Experiments on ringing or girdling of pear shoots showed results which waited full many a year for adequate explanation. He saw that the margin of bark above the decorticated ring swelled,

but that the margin below showed no increase. He concluded that the difference was due to the interruption of the flow of nutrients and to their accumulation in the upper margins. He also observed that a narrow band of cortex isolated by girdling lived and regenerated if it contained a leaf bud, but not otherwise. His figures leave no doubt of his perception of something of great physiological import.

Although MALPIGHI had announced that leaves were concerned with nutrition and that respiration was a universal process in plants as well as in animals, he let the matter stand there. HALES contributed to the solution of the question by his conclusion that leaves were of primary importance because they acquired some part of the plant's nourishment from the air. He remarked that "air makes a very considerable part of the substance of vegetables". HALES' work on assimilation was nothing but a very modest beginning, but it showed that he was far ahead of his contemporaries. Quantitative studies on the growth of shoots and leaves initiated by HALES showed that there were gradients, *i.e.*, the apical region of the vine was the most actively growing region. HALES will ever be remembered both for his remarkable discoveries and for the introduction of quantitative methods into plant physiology. SACHS said about him, "HALES had the art of making plants reveal themselves. By experiments carefully planned and cunningly carried out he forced them to betray the energies hidden in their apparently inactive bodies".

The scientific heights reached by HALES were not maintained for long. In the half century which followed the publication of "Vegetable Staticks" plant physiology fell back into a state characterized by poorly planned experiments and illogical conclusions which misled others and fostered pernicious errors which were not soon eradicated.

The Swiss entomologist CHARLES BONNET (1720-1793) advanced certain preposterous ideas about leaves. His book "Recherches sur l'usage des feuilles des plantes" (1754) launched a host of misconceptions about the ability of leaves to absorb dew and rain water. Admitting that water escapes from leaves during the day, he assumed that no transpiration occurred during the night and that the sap then returned to the roots and, furthermore, that water vapors, rising from the earth and condensing on the lower sides of the leaves, were sucked into the plant and conveyed to the stem. BONNET never displayed his sophistry more plainly than when he claimed that this vapor-capturing function was an adequate explanation for the heliotropic and geotropic movements of leaves.

The French dendrologist DUHAMEL (HENRI LOUIS DUHAMEL DU MONCEAU, 1700-1781) experimented, in company with BUFFON and independently, in animal and vegetable physiology. He was also interested in nautical matters and during the latter part of his life was engaged as inspector-general of marine for the Channel district of the French coast. His botanical work may be regarded as the inception of forest botany. DUHAMEL's "La physique des arbres" (1758) is a two-volume work in which he summarized the work of HALES and others and recorded as well much that had been known by gardeners and foresters. An air of medievalism often tinges his explanations of experimental work. He

adopted BONNET's ideas about leaves, but paid much more attention to their anatomy. He perceived that the heliotropic curvatures of leaves were conditioned by light, but could not understand why movement of *Mimosa* leaves occurred in the darkness. His ideas on the functions of leaves are far inferior to those of HALES.

DUHAMEL's observations and experiments on the organization and growth of woody plants were far more successful, though his descriptions are extremely prolix. He decorticated trees and observed the regeneration of new cortex when the exposed areas were covered to prevent desiccation of the wood. He inserted silver wires horizontally into tree trunks (1) between the wood and cortex as well as (2) in the cortex. He found that in (1) the wires became embedded in the wood; in (2) they were pushed out and remained in the cortex. From these and other experiments DUHAMEL concluded that cortex is not converted into wood, but that wood grows by the addition of new layers which arise from a gelatinous layer between wood and cortex. His numerous experiments on girdling trees and observations on their anatomy seem not to have given a more precise idea of the cambium.

His discussion of the action of fertilizers on plants was a repetition of what the gardeners and orchardists of his time knew. His ideas on plant nutrition betray much that was Aristotelian in conception. DUHAMEL's discussions of the diseases of trees, though of little scientific value, have great historical interest. He observed that sometimes insects or extremes of moisture or temperature produced injuries which greatly affected the life of the tree. The fact that he attempted to relate diseases to assignable, material causes merits our attention, although he had little to offer in the way of prevention or cure.

JOSEPH PRIESTLEY (1733-1804) is famous for the discovery of oxygen and of its production by plants. He was educated for the clergy and served in several parishes in England. He pursued chemistry as an avocation, but his experiments uncovered fundamental facts and his results were recorded with clarity and accuracy. While he was a tutor at Warrington academy he wrote the "History and Present State of Electricity" (published 1767) which cemented his friendship with BENJAMIN FRANKLIN. Its publication was the occasion of the author's election to the Royal Society. His fame as a chemist rests upon his publication "Experiments and Observations on different kinds of Air" (1774, 1775, 1777). In 1774 PRIESTLEY, by heating mercury monoxide, obtained gaseous oxygen, the fundamental properties of which he described and called "dephlogisticated air". Later LAVOISIER gave it the name which has since been used.

PRIESTLEY had noticed in 1771 that plants confined in an atmosphere rich in fixed air (carbon dioxide) produced in the course of several days large quantities of dephlogisticated air (oxygen). He concluded erroneously that the process was due to the growth of the plants. His work was concerned with the chemical changes in air and he was interested solely in the effects that plants had upon air and not at all in the reciprocal influence of air upon plants. His discovery, nevertheless, was so fundamental and opened the way to so many subsequent fruitful investigations that his work may not be disregarded. SCHEELE, a Swedish chemist, undertook a study of this function of plants and obtained

results which contradicted PRIESTLEY's conclusions. He found that plants produced carbon dioxide instead of oxygen, but he had not given them sufficient illumination. PRIESTLEY repeated his experiments, obtaining irregular and confusing results; he eventually abandoned further work on the problem. He never discovered the role of light in the production of oxygen by plants. PRIESTLEY's discovery of oxygen, however, which was to play an important part in the New Chemistry founded by LAVOISIER, not to mention his observations on the exhalation of oxygen from green plants, surely entitle him to recognition in the scientific world. (Fig. 30).

PRIESTLEY may be considered a pioneer in the progress of man's emancipation from the realm of mysticism and fantasy. He was a sincere seeker after truth, and, although violently partisan, a man of irreproachable character. He was an extreme radical both in religion and politics. Endless strife and personal persecution were his lot. His home having been mobbed and pillaged, he escaped with his life and fled to London. Finding nothing but opposition and strife there, he fled to America and settled at Northumberland, Pennsylvania, where he spent the rest of his life. He declined the offer of a professorship of chemistry in Philadelphia, and later of the principalship of the University of Pennsylvania.

Knowledge of the activity of plants in changing the composition of air, was immensely increased by JAN INGENHOUSZ (1730-1799), a Dutch physician who also had wide scientific interests and knowledge. In many ways the personality of INGENHOUSZ was a counterpart of PRIESTLEY's. He came from an affluent family, well educated, a favorite of royalty, and a conformist in social and religious matters.

INGENHOUSZ was educated for the medical profession and practised for six years in the Netherlands. Although a busy physician, he seized every opportunity to prosecute scientific studies in physics. In 1765 after the death of his father, INGENHOUSZ migrated to London where he became a member of a group of distinguished scientists. He was called to Vienna to serve as court physician on account of an epidemic of smallpox of unwonted severity which had claimed as victims several members of the Royal family. He remained from 1768 to 1779 in Vienna where he achieved great success in immunizing patients by vaccination, then returned to London.

Stimulated by the discoveries of PRIESTLEY, INGENHOUSZ began again to study the relations between air and plants. His essay, "Experiments on vegetables" (1779), reported that the growth of plants had nothing to do with the purification of the air, that they were able to purify the air only when they were exposed to sunlight, under such conditions they absorbed air and exhaled oxygen, and that this function is more active in bright sunlight than in the shade, and that at night, contrariwise, they vitiate the air as animals do. His demonstrations of the dependence of oxygen formation upon light solved the problems which baffled PRIESTLEY. He sketched in its outlines the cycle of carbon in nature, showing the interdependence of plants and animals, since air rendered unfit for breathing by animals is purified by green plants in the light.

Time and again INGENHOUSZ speaks of "bad air", meaning air which is unfit for animal respiration, showing thereby that his interest in the action of green plants was due to their power to

"purify" the air. He also discussed the value of green plants in dwellings and the species of trees which should be planted in gardens. He decided that plants in living rooms were detrimental to the composition of the air unless they were always exposed to the sun light. INGENHOUSZ did not advance any idea about the component of "bad air" which was removed by the plant; his interest seems to have been directed to the phenomenon of purification of air and its relation to animal life. Be it remembered, however, that he worked on these problems before LAVOISIER had established the composition of carbon dioxide and the nature of combustion. INGENHOUSZ was no more a botanist than PRIESTLEY, he was a physician and physicist who by untiring work and splendid intelligence gave a directive influence to plant physiology. He was not content until he had made exact measurements of the gases evolved by plants thereby laying the foundations, as HALES had done, for quantitative work. HALES had given very plain intimations that some important part of the nutritive substance of the plant is derived from the atmosphere, but INGENHOUSZ, although stating in the preface to his book that the purification of the air serves the plants as some kind of nourishment, did not definitely advance knowledge of the subject. The physiologist feels inevitable disappointment that INGENHOUSZ did not pick up the thread where HALES dropped it.

INGENHOUSZ returned to the problem of nutrition subsequently and reinvestigated it after LAVOISIER had discovered the composition of carbon dioxide. We find the new ideas discussed in INGENHOUSZ' "Essay on the Food of Plants and the Renovation of Soils" (1796), transmitted to the British Board of Agriculture. In this "Essay" we find a growing belief that carbon dioxide is absorbed by the plants, but its author is not clear as to whether all is absorbed by leaves or partly by roots. Since organic manures added to the soil disengage a great quantity of carbon dioxide, it seemed probable to him that the principal attention in manuring ought to be directed to the time of applying it to the soil. If it is applied when it is in the height of its putrid fermentation, the growing plants may absorb the "fixed air", or carbonic acid, either in a nascent state, or as it is being incorporated with various salts and earths which are to be found in almost all soils.

INGENHOUSZ made some pertinent observations on the liberation of carbon dioxide from soils. "All this shows in a manifest manner", he said, "that the soil draws incessantly from the incumbent air the oxygen, the general acidifying principle". He could not know that micro-organisms were responsible for most of this oxidation. Yet, he saw that siliceous sand, either dry or moist, does little or nothing at all to injure the air over it; nor is it materially affected by being shut up with pure water. He suggested that farmers add acids to the soil, since his experiments with them produced increases in plant growth.

JEAN SENEBIER (1742-1809) made further advances in physiology and wrote the first general treatise on the subject (Physiologie Végétale, 5 vols., 1800). SENEBIER, born in Geneva, was minister of the church of St. Evangile and city librarian. A revolution in Geneva drove him to the Canton Vaud, where he wrote the treatise mentioned above, but in 1799 he returned to Geneva and participated in a new translation of the Bible. He also trans-

lated the important writings of SPALLANZANI, studied chemistry under TINGREY, and investigated the physics of light. All in all, he was extremely conversant with the scientific literature of his time and had a literary skill adapted to the readers of his day. SENEBIER's important contribution to physiology was "Expériences sur l'action de la lumière solaire dans la végétation" (1788) in which he critically reexamined all that PRIESTLEY and INGENHOUSZ had done. He was seldom satisfied with the results of a single experiment, but repeated it with a different plant or under somewhat different conditions. In so far as possible, quantitative methods were always employed. He used algae and subaquatic plants as well as the cut branches of herbs and trees. The results were meticulously compared and, whenever possible, differences were explained, sometimes he admitted that the results were inconclusive.

He proved that light, not heat, is the effective agent in the fixation of carbon dioxide and that oxygen is only liberated when carbon dioxide is present, but he advanced no further. He regarded light as a flood of corpuscles which escape continuously from the sun, *i.e.*, a form of matter which entered into combination with bodies which they struck. "It appears from my experiments", he wrote, "that the light decomposes the fixed air in the leaves". SENEBIER characteristically tried to relate the events observed by him to physical and chemical processes, thus severing the age-long tie with Aristotelian biology. He discussed INGENHOUSZ' work at length, with much of it he was in agreement, but with some he differed. Working at a later date, he was better equipped than INGENHOUSZ with chemical knowledge.

The development of plant physiology in the 18th century is truly significant. The speculative efforts of the predecessors of the investigators of this period were abandoned and experimental researches initiated. One must be conscious of the effects of Newtonian physics and, towards the end of the century, of the dawn of the new chemistry. The atmosphere was charged with new and stimulating ideas which changed men's outlook on the universe. If biology seemed to lag behind astronomy and physics, it is but another instance in which the difficulties of scientific examination of sentient organized beings have baffled investigation.

Botanical exploration in the 18th century:- JUAN DE LOUREIRO (1715-1796) was one of the most devoted students of the southeastern Asiatic flora who went out from Europe. After his arrival as a Jesuit missionary in Cochinchina, he apparently gained influence for we find him holding office at the court of the king. His slight knowledge of medical arts rendered him very popular among the people. Since European medicines were not within his reach, he was forced to depend entirely on native drugs and by investigating them he was led to study the flora of the country and to make botanical collections. Thus he accumulated a good herbarium of approximately 1000 species.

He was not a professional botanist but had acquired good botanical knowledge to whom we owe one of the most important contributions concerning the flora of the eastern part of the trans Gangetic Peninsula and of South China.

In 1790 LOUREIRO proceeded to Canton where he continued his botanical researches for three additional years. Although foreign-

ers living at that time in Canton were not allowed to walk beyond the limits of the factories, LOUREIRO hired a Chinese peasant, acquainted to a certain degree with the medicinal plants of the country, to make collections for him. This Chinaman communicated also the common names of the plants. Since there appeared to be some discrepancies in the names, LOUREIRO obtained a good Chinese work on botany and not only verified all names given him, but also spelled the names in his Flora Cochinchinensis according to the Mandarin dialect.

LOUREIRO seems to have embarked with his collections in 1782 stopping for three months on the island of Mozambique where he collected more specimens. In Portugal, his native country, he spent several years preparing for publication his botanical work "Flora Cochinchinensis" (1790).

MICHEL ADANSON (1727-1806) was a traveller-naturalist who possessed to an extraordinary degree the zeal for explorations. Having enjoyed the best educational opportunities that Paris afforded and attracted the attention of men like RÉAUMUR and CUVIER, he was well fitted for a scientific career. This brilliant, but enigmatical, character in 1748 gladly embraced the opportunity to go to Sénégal in west Africa. It was a very modest position as far as remuneration was concerned, but ADANSON was young and full of zeal, and positions in France were already filled with older men.

It is not easy to describe the fervor with which young ADANSON embarked on this trip. CUVIER in writing about it said, "The motives of his decision for Sénégal are curious. It is of all the European establishments, the most difficult to penetrate, the hottest, the most unhealthy, the most dangerous in all respects, and, as a result, the least known to scientists". In later years ADANSON confessed that it took a great deal of courage to undertake single handed a task which ordinarily demands the collaboration of a botanist, a physician, an anatomist, and a draughtsman, but these considerations daunted him not at all.

ADANSON reached Sénégal in April 1749 and remained four years and four months making an inventory of the natural resources of the country for the India Company which had established trading posts there. He found, and one can imagine with what satisfaction, that most of the animals and plants he saw were not even mentioned in the books that he had studied, for the very good reason that men of science had never seen any of them. He set out to study and classify them, eager to know their affinities and to establish their relationships with animals and plants that he had formerly studied in France, either in the cabinet of RÉAUMUR or in the Jardin Royal. In addition to collecting, classifying, and preserving specimens, ADANSON was elaborating little by little his natural system of classification. From Sénégal he wrote in 1750 to BERNARD DE JUSSIEU announcing his system. "Histoire naturelle du Sénégal" (1757) and "Familles des Plantes" (1763) which he published after his return to France, represented the results of his surveys of Sénégal. Out of his jungle experiences ADANSON evolved another idea much in advance of its time, namely, the mutability of species. Although crudely and imperfectly formulated, this idea preceded LAMARCK by forty years and DARWIN by nearly a century. ADANSON's ideas were

received with hostility by inferior rivals who should have fostered them, and years passed before anyone took up his unfinished work. The work of explorer, taxonomist, systematist, philosopher, and encyclopedist has rarely been so perfectly accomplished by one man.

Sir JOSEPH BANKS (1743-1820) was by all odds the most extensive and intrepid botanical explorer of the 18th century. It is said that his early interest in botany was kindled by reading a copy of GERARD's Herball which he discovered among his mother's books. His zeal for collecting plants was unsurpassed, but he had no great ability as a writer or interpreter of botany.

In 1766, after having been elected a fellow of the Royal Society, he began his travels by a trip to collect plants in Newfoundland and Labrador whence he brought the first scientific collections to England. Shortly thereafter BANKS joined Captain COOK who was then preparing for his voyage around the world, accompanied by Dr. SOLANDER, friend of LINNAEUS, and two artists. They visited Rio de Janeiro, Cape Horn, Tahiti, New Zealand, Australia, the Malay Archipelago, Cape of Good Hope, and St. Helena, bringing back plants collected in these regions. During the visit to Tahiti, BANKS sowed seeds of various Brazilian plants. The expedition, apart from its geographical results, rendered great service to botanical science in the accumulation of specimens of the greatest value and importance. In 1772 he explored the Hebrides and Iceland, and discovered the great geysers of the latter country. His great collections and library, now preserved in the British Museum, are accessible to naturalists of all countries and form the basis of many important systematic works. It is clearly impossible to relate all the expeditions which brought back to Europe a wider scientific view of the flora of the world in the 18th century. All of them; travellers, collectors and systematists, laid the foundation for the science of phytogeography which had a remarkable development in the 19th century.

This glimpse of botany in the 18th century, which is confessedly fragmentary, may suffice to show that the science was undergoing a restless development. The compact sod which covered many a field of thought was broken and overturned. The century was a time of criticism, and agnosticism in intellectual life. Mixed with the garnered grain there was much chaff. The natural sciences had not then begun to consolidate their gains. With the exception of the central European states, the vested interests of church and state were indifferent, to say the least, to scientific progress. Notwithstanding the resistances of the philosophical and political strongholds of the day the plant sciences made conquest of new territories from which they have never been forced to retreat.

REFERENCES:

CLARK-KENNEDY, A. E. (1929): STEPHEN HALES. University Press, Cambridge.

GREEN, J. R. (1914): A history of botany in the United Kingdom. Dent, London; Dutton, New York.

HAWKS, E. (1928): Pioneers of plant study. Sheldon Press, London; Macmillan, New York.

JACKSON, BENJ. D. (1923): LINNAEUS . . . the story of his life, adapted from the Swedish of T. M. FRIES. Witherby, London.

LOUREIRO, JUAN DE (1790): Flora Cochinchinensis. 3 vols. Ulyssipone. (German transl. 1793 by C. L. WILLDENOW, Berlin).

NORDENSKIÖLD, E. (1928): The history of biology (transl. from the Swedish by L. B. EYRE). Knopf, New York and London.

PEATTIE, D. C. (1936): Green Laurels. Simon & Schuster, New York.

RENDLE, A. B. (1904-1925): The classification of flowering plants, 2 vols. University Press, Cambridge.

ROBERTS, H. F. (1929): Plant hybridization before MENDEL. University Press, Princeton.

SACHS, J. VON (1890): History of botany (1530-1860) . . . authorized transl. by H. E. F. GARNSEY . . . rev. by I. B. BALFOUR. Clarendon Press, Oxford.

SCHMUCKER, T. (1936): Geschichte der Biologie. Vandenhoeck & Ruprecht, Göttingen.

Chapter VIII.

GARDENS AND OTHER THINGS.

The importance of certain cultural relationships fragmentarily sketched in foregoing chapters must now be more specifically discussed.

On preceding pages I have narrated how GERARD and PARKINSON based herbals on the plants cultivated in their gardens; how PHILIP MILLER and HENRI DUHAMEL studied acclimatization and growth; and how JOHANN GLEDITSCH and RUDOLPH CAMERARIUS made experiments on pollination in their gardens.

The business of gardening influenced the development of the plant sciences in untold ways through the arts of selection, domestication, and cultivation. It also ministered to the study of plant taxonomy, hybridizing, medicinal properties, and food values. A garden is a bit of land where certain natural tendencies are isolated from others and given fuller expression. There would undoubtedly have been a greater lag in the plant sciences had it not been for the development of public and private gardens, and the interests they engendered. They sent many a person to the woods and fields for seeds and fruits, and not a few to foreign lands for new botanical treasures.

Roman Gardens:- The ancient Romans, who were noted for their predatory conduct toward other tribes and peoples, as well as for an absence of scientific ability, pilfered, extorted, plundered, or despoiled other lands of fruits, grains, and vegetables which, through centuries of toil, had been tamed and bred. The luxurious Roman villas, each surrounded by exquisitely beautiful gardens, were characteristic of the unwonted extravagance of the Augustan age. Gradually the size of the gardens was increased, the expensive decorations multiplied, and picturesque scenery developed, as one may see today at Tivoli. PLINY was interested in market gardens and the cultivation of medicinal herbs. In opposition to the gluttonous and extravagant mode of life of his time, he extolled the garden as a means for acquiring a rational mode of life and a source of healthful, nourishing food. The cultivation of a plot of ground where food plants were grown was one of the important duties of the slave's husky wife. PLINY's practical mind was more interested in the utilitarian than in the esthetic aspects of gardening. Flowers, though beautiful, were fragile and soon faded; culinary and medicinal herbs really ministered to the needs of humanity.

The craze for novelties and out-of-season viands for the sated appetites of the Roman overlords compelled the gardeners to invent methods for forcing, and ingenious tricks in cultivating exotic plants. Accurate reports of the methods employed were not published, naturally enough; on the other hand, there were oft-

FIG. 17. — Gardening scene from "Les occupations des mois". Grandes Heures de Rohan, 15th century. The Master Gardener wielded the pruning hook and his servant the mattock. From a copy in the Bibliothèque Nationale, Paris.

repeated statements of magical incantations of reputed efficacy, many of which have been recorded and transmitted to the present time.

Regardless of the methods employed, we know that the Romans succeeded, often at great expense and labor, in assembling and cultivating in their country more new sorts of food plants than any other people had acquired. Apples, pears, and plums came from Greece, Armenia, Numidia, and other places, the peach from Persia, the fig, olive, and almond from Syria. PLINY mentions twenty-two kinds of apples, eight of cherries, three of quinces, and so forth, indicating that as the years went on the gardeners selected out new varieties of the fruits introduced. The Roman officials in charge of colonial outposts were seldom interested in ameliorating conditions for the inhabitants, but a few encouraged Roman settlers to transport, and plant, vines and trees. By the third century A.D.,

FIG. 18. — De area (flailing grain) from P. CRESCENTIIS, De Omnibus Agriculturae Partibus et de Plantarum . . . Basil, 1548.

the apple is known to have been introduced and cultivated in the British Isles.

North European gardens:- During the Dark Ages in Europe, it is not surprising that there was little attention paid to introducing and planting new fruits and vegetables in the gardens. From the time of CHARLEMAGNE gardens and orchards were mentioned as a part of the property of monasteries and other religious houses in northern Europe. As the size of the monastery grew, due to the influx of young men, it became desirable to enlarge the gardens to provide food, as well as employment, for the members of the religious house. In many cases monks were able to bring trees and plants from the home of the Mother Church in Italy and to cultivate them in the new environment. Moreover, when marauding armies devastated countries, the properties of the church were generally spared, and consequently many varieties of fruits and vegetables survived which would have become extinct

if grown on unconsecrated soil. The number of vegetables grown for food was not large; however, they had spinach and other "greens". The former, carried northward from the Mediterranean countries, had become a half-wild thing, carelessly cultivated, and often trodden under foot of man. Then there was the "Good Henry" (*Chenopodium Bonus-Henricus*), which, though uncultivated, jumped the garden walls and led a precarious existence, growing tenaciously between paving stones and in fields along the pathways.

The gardens of the Benedictine monastery of St. Gall, near the Lake of Constance, were described in a "Bauriss" compiled in 820 by one who had evidently written the plant names from memory in his old age, and made no attempt to separate medicinal from culinary plants. Moreover, many vegetables in current use were altogether omitted. Since he told how they were arranged in the garden, we can surmise that he had been the gardener. He told

FIG. 19. — De his quae (graftage) from P. CRESCENTIIS, *op. cit.*

of lilies, roses, mints, and fenugreek (the Greek hay) in one bed; in "The Herbularius" there were sage, rue, gladiolus, and cummin; in the vegetable garden, "The Hortus", there were onions and garlic, dill and beets, parsnips and cabbages. It is worthy of note that the preponderance of plants was of Mediterranean origin, brought thither, perhaps, by itinerant monks.

The North Europeans neither discovered nor domesticated any important indigenous crop plant, but they were adepts at receiving and cultivating exotics. In the early days their diet during much of the year must have been monotonous, to say the least, and conducive to the liberal use of alcohol to stimulate a jaded palate.

When once the appreciation of Italian gardens had crossed the Alps, it awakened in northern Europe a lively enthusiasm for the art of gardening. The Renaissance brought a notable widening of the horizon of men's minds, and the sixteenth century herbalists made the world acquainted with a vast number of plants. Never-

theless, the supply of plant material for gardens was scanty until after 1600. Apparently there had been few attempts to that time to domesticate and select plants for gardens. In certain respects the north European gardens in the time of the Renaissance were modelled after the Roman gardens, but they often included bowling alleys, or fountains, and perhaps mounds. In one respect they were similar — in attempting to isolate the portion of ground devoted to the gardens. Fences and walls were built to imprison the vegetables and flowers, each in their proper place, thereby often obscuring plants, except the tallest. Walls of clipped trees of cypress, or of yew, were sometimes substituted for masonry. They eventually curved and curled the walks into mazes and labyrinths, making knot gardens in ultra-baroque patterns. Geometrical symmetry was the rule. Fruit trees were sometimes planted within and bordering the garden walls, and eventually were pruned to

FIG. 20. — De allio (onion) from P. CRESCENTIIS, *op. cit.*

permit them to be supported by the walls. The Italian influence in Elizabethan times was suited only to large gardens. Garden construction and planting followed the concomitant increase in private wealth, no less than they followed the northward spread of other arts and sciences.

The establishment of university botanical gardens in 1533 at Padua, in 1547 at Bologna, in 1560 at Zürich, in 1570 at Paris, in 1542 at Leipzig, in 1621 at Oxford, was the means of disseminating knowledge of plants, which had formerly been confined largely to printed books. The botanical garden of the University of Leiden owed its initial development to CLUSIUS who obtained many new plants by exchange and from explorers. The impulse given to botanical study by the establishment of gardens at centers of learning seems perfectly natural. Both the scientific and the culinary garden were places where plants were tested and examined. The better one knew the native climate, soil, and habits, the better the results he would obtain. Although printed records are scarce, some information about the garden plants may be gleaned from a study of the paintings of the day, especially those of the Dutch School.

Post-Renaissance Developments in European Gardens:- Inspired by a desire to make the gardens as complete as possible and to beautify the environs of their homes, there was in all the countries of Europe, in post-Renaissance times, a mounting interest in the plants brought from other countries, following the era of discovery and colonization. Tobacco and tomatoes were originally grown as ornamentals in the flower gardens, along with the small fritillary, which was at that time designated the "Turkie" or "Guinihen" flower, or "Checkered Daffodil".

The discovery of the beauty and earliness of exotic flowers in English gardens was clearly set out by JOHN PARKINSON in his Herbal, published in 1629. He said, in that work, that these flowers blossomed so early in the year that they seemed to make the garden a delight even in the winter time, lasting until indigenous flowering plants come on. In his discussion, he evidently had in mind the gentry and nobility of his country, who could afford to buy exotics. Tulips were carried from Holland to England early in the reign of Elizabeth, being taken in all probability by the Flemish cloth-makers who fled the persecutions of PHILIP II and the Duke of ALBA in 1667. The volume of imports is indicated by PARKINSON's mention that they had almost a hundred sorts of daffodils, both single and double, and about half as many hyacinths. The list of other exotic plants in his discussion includes almost exclusively south European plants. The indigenous plants which had been domesticated and utilized for flower gardens included violets, columbines, primroses, and cowslips. He sagaciously remarked, however, that many of the so-called "native" plants were actually brought to England a long time previously and cultivated so long that the memory of man ran not to the contrary. He had some trenchant statements about survivals and acclimatization of the introductions and, consciously or unconsciously, hit upon some important concepts in adaptation, dormancy, and growth. In all that he said about the culture of indigenous or exotic plants, he gave reasons which he learned from experience, omitting all the old-time superstitions and fairy stories. Gardening and the pharmacopeia had begun to emerge from the erstwhile domination of sorcery. When he knew of no beneficial medicinal properties, he said so, though adding that claims for the same had been made in former times.

It is difficult to say when gardening became a national recreation in England and Scotland, but apparently it antedated the founding of the Royal Society, or the creation of the Chelsea Physic Garden. Writers in the 17th century presented various ethical, practical, medicinal, and spiritual reasons for gardening, but one suspects that these were merely pretexts for doing something they loved to do, and would have done anyway. Londoners as early as the twelfth century seemed to have some gardens of pretension, though it is probable that the most important parts of them were the walls and fountains.

The tulip and its cultivation in Europe is a notable example of a mania for garden-flowers which stimulated an interest in the breeding and selection of varieties by amateurs. The Turks, from whom European tulips were obtained, had cultivated the plants for an unrecorded time. GESNER saw the plant for the first time at Augsburg in 1559 and described it with a figure. In Holland,

the craze which began in 1634 for tulip breeding and selection reached such a pitch that governmental intervention was eventually necessary to stop the wild speculation. DUMAS' "Black Tulip" gives an interesting picture of the tulip mania. CLUSIUS, who had propagated tulips on a large scale in Holland, described (1576) the plant and published a picture of it. He introduced tulips into England about 1577, where they were popular for a time, although eventually superseded by other introductions from the Americas and South Africa. LA QUINTINYE listed 416 named varieties of tulips in 1697. The early pictures of tulips show many varieties, with flower segments (at least the outer) acute. The broad, rounded, erect petaled forms were developed by the Dutch gardeners and produced wholly by selection. The "Breaking" in the color of the tulip flower, described originally by CLUSIUS, is now ascribed to a plant virus. Double tulips made their appearance at an early date in Holland and continue in cultivation.

Immigrant plants began to arrive in the sixteenth century. Austria, under the stimulus of CLUSIUS and JACQUIN, was the portal through which foreign plants entered. FRANCIS I, Emperor of Austria, encouraged the introduction of exotics, and sent out a notable expedition in 1754 which brought home plants which formed the basis of the beautiful Schönbrunn gardens. Plants from the Atlantic seaboard of North America were not widely grown in Europe until after the founding of English and Dutch settlements. Their introduction then followed so rapidly that by the year 1700 there were 150 American plants in cultivation in Europe, and their numbers continued to increase until the time of the Revolutionary War. The disruption of travel and communication by the contemporary wars is graphically set forth in the letters of botanists in the 18th century. There is no way of knowing how much valuable material and labor was lost through acts of vandalism, shipwreck, and war, as shown by two excerpts, *viz.*, ALEXANDER GARDEN to JOHN ELLIS, July 6, 1757.

> "My grief at my own and your disappointment is inexpressible. A few days ago I heard that both Capt. COATS and CHEESEMAN were taken, and with them the two most valuable collections of seeds that ever I could promise or even hope to procure for you . . . Good God! what is the meaning that out of 21 Carolina ships that sailed from hence in January last and the beginning of Feb. there should be 19 taken, and with them no less than five hundred thousand weight of our best Carolina indigo."

JOHN ELLIS to C. LINNÉ, London, Dec. 21, 1762.

> "Now that we are to have a peace, I shall extend my correspondence, and hope to meet with many new discoveries; which, if I do, shall immediately communicate them to you."

The importation of forest trees, tardily undertaken, was an addition to English and French gardens in the eighteenth century. The value of the exotic trees which had found their way to England was discussed by MARK CATESBY in his "Hortus Brittanico-Americanus", and the physiology of trees by DUHAMEL in "La Physique des Arbres" (1758). PHILIP MILLER discussed *Magnolia grandiflora,* stating that it had been planted in England before 1739, although the majority of the trees were destroyed by the severe winter of that year. He said, "If this tree can be so far

naturalised as to endure the cold of our severest winters abroad, it will be one of the greatest ornaments to our gardens . . ." EVELYN's diary contains frequent allusions to arboriculture, and his "Sylva" recommended species to be planted. Through British officials in the New World, EVELYN secured seeds and, sometimes, seedlings of forest trees and shrubs of New England and Virginia, including cedars, pines, oaks, maples, etc. His directions (dated 1 sepr., 1686) for the preparation of shipment of trees are worth quoting:

> "The trees in Barills their rootes wrapped about mosse: The smaller the plants and trees are, the better; or they will do well packed up in matts; but the Barill is best & a small vessell will containe enough of all kinds labells of paper tyed to euery sort with ye name . . . "

A goodly collection of Virginia trees was carried to England and planted by the younger TRADESCANT at Lambeth where some of them reached a high degree of perfection, among them the Tulip-tree, on which EVELYN commented favorably.

In the 16th, and still more in the 17th, century there was a ventilation of men's minds. More new thoughts came to them than in almost all of the preceding two thousand years. Even a grimy gardener would straighten his bent back and rub his eyes to see a new plant from the outside world. No less a personage than Sir FRANCIS BACON, who started a train of new thought which apparently will have no end, shifted men's eyes to the magnitude of the living universe about them.

If there was less reverence for the authority of DIOSCORIDES and PLINY, there was no whit less reverence for Holy Writ, as shown by the fact that about one garden book in every three had copious references to the Garden of Eden or to the choice plants which must have been cultivated there by Adam and Eve while they were still in a state of purity and innocence. WILLIAM COLES' quaint book called "Adam in Eden", published in 1657, was characterized by its subservience to classical authors, showing how hard it is for the human mind to free itself at once from all the chains which bind it to the conservative ideas of the past. In the same vein of thought, the liberal use of the word "Paradise", the abode of the blessed, came into garden literature. The idea of a Paradise of Flowers, in JOHN PARKINSON's famous "Paradisi in Sole", implied a better condition of body, mind, and soul resultant from the maintenance of a good garden, a belief which probably appealed strongly to the bewildered world of their day.

RICHARD BRADLEY's practical mind was occupied with kitchen gardens, physic gardens, and nurseries for the propagation of trees. He praised the kitchen gardens of England for the variety and quality of their produce, but condemned the French gardens because they had little more than herbs for fruits and salads. He was charmed by the abundance of exotic plants in the physic gardens at Amsterdam, where plants had some sort of classification, and where the professors COMMELIN and RUYSCH read to the citizens twice every week. Gardening in Holland had already begun to benefit from the commerce with the East and the West Indies.

The beginning of the Royal Botanic Garden at Kew was rather casual. If the date 1760 be accepted for the foundation, it must be admitted that even the royal patronage did not produce any

remarkable results. When, after the death of the queen who had sponsored the garden, Sir JOSEPH BANKS assumed charge in 1772, the development of the gardens on a scientific plan began. Botanical collectors were sent overseas for plants. King GEORGE III and his queen encouraged the project; for a time everything went well, but misfortune befell it later, and things went badly until 1841 when Sir WILLIAM JACKSON HOOKER was appointed director. In the succeeding century the garden and herbarium made remarkable advances in many lines, becoming a great international center of research and dissemination of knowledge.

Plant Introductions:- A few parties went out at this time in search of new plants for the fields and gardens. Among them, JOHN TRADESCANT, who was born about 1570 and died about 1637, is thought to have made a journey to Russia in 1618. It is quite definitely known, however, that in 1620 he voluntarily joined an expedition against the pirates of Algiers. We shall probably never know what his life was like while they were slaying Saracens on the Barbary Coast, or where they landed, or how much of the time Brother JOHN used his trusty sword to uproot native plants. At any rate, he brought back with him a variety of apricot which was commented upon by JOHN PARKINSON in the following words: "The Argier Apricotke is a smaller fruit than any of the other and yellow . . . This with many other sorts JOHN TRADESCANT brought with him returning from the Argier voyage, whither hee went voluntary with the fleete that went against the pyrates in the yeare 1620." Having returned from this adventurous trip, TRADESCANT became the Royal Gardener. He established a physic garden at South Lambeth, and was the first Englishman "who made any considerable collection of the subject of natural history". His son JOHN (1608-1662) added largely to his father's collection, and, in 1637, visited Virginia, where he collected flowers, plants, shells, and so forth.

One of PARKINSON's associates was WILLIAM BOEL (BULL), a native of the Low Countries, who traveled and collected in Spain and Portugal (1608), in Tunis and in Barbary. PARKINSON's comments are interesting, even though at variance. In one place he speaks of BOEL as "going into spain almost wholly on my charge, but bringing me little else than seedes of Chiceling Peas for my money". Yet he gave the seeds to others, so that "I beate the bushe and another catcheth and eateth the birds". However, at another place PARKINSON says, "He gathered about two hundred sorts of seedes . . . all of which I had my part and by sewing them saw the faces of a great many excellent plantes, but many of them came not to maturitie with me, and most of the others whereof I gathered back seedes one yeare by unkindly yeares that fell afterwards have perished likewise".

Still men explore for plants. Out where there are unclimbed mountains furrowed with green valleys, the explorer flirts with death to court some dainty beauty of a *Primula,* or revel in the ravishing radiance of a *Rhododendron* in flower.

Pleasant to read in the lap of an arm-chair are the romances of plant hunting, because their writers relate chilling, bruising climbs, alternating with strenuous trips through steamy-hot, leech-infested jungles in search of something rare. Who would not de-

light to read again the journal of DAVID DOUGLAS, who perversely went alone on his searching expeditions, until he met a gruesome, tragic death in Hawaii; or of NUTTALL, "Old Curious, the sailors called him", whose eagle-eye missed nothing, who used the barrel of his musket as a receptacle for the seeds he collected?

To look at the names of some genera of plants is to reincarnate some botanist like BARTSCH who, at LINNAEUS' request went out to Surinam where he died within a few months. The following excerpt, apropos of a new genus, contains LINNAEUS' eloquent appreciation of the man:-

"I have called it *Bartsia* for JOHANN BARTSCH of Königsberg, doctor of medicine, a well-favored, straight-forward youth, and unquestionably most learned, a credit to his country. I formed his intimate acquaintance in Belgium, and inspired in him an invincible passion for plants and insects to such a degree that he had few superiors in examining the minutest parts of plants and describing them with great acuteness. The position of doctor-in-ordinary to the Belgian Society of East India falling vacant, the immortal BOERHAAVIUS chose me for Surinam; when however I declined to make my home in the torrid zone, a child of the North by birth and training, that man of blessed memory granted me the privilege of nominating for the post whomsoever I wished. This proposition delighted my honorable friend BARTSCH for no other reason than that of the plants. He was recommended to BOERHAAVIUS, was accepted, and sailed for Surinam. There, because of some inexplicable hatred and ill-will on the part of the governor of Surinam he never enjoyed a single happy hour; as a result he died six months later, the victim of ennui, dislike, poverty, and heat, though if ever a man deserved a better fate it was he. The character of the man is evidenced by his Dissertation on Heat and by his letters dispatched to me from Surinam, full of the most interesting observations on plants." (Translated by Professor W. H. ALEXANDER).

In later years there were men like FARRER who climbed the Stone Mountains on the eaves of the world in Asia, where he found *Primulas* and *Rhododendrons*. In Szechuan he found a few sere, dried out plants of a *Primula* after a long day's climb over the rock-faced hills. The discovery kindled all the emotions of a hunter in him, and impelled him to explore all the chaffy capsules on the brown stems. The small pinch of seeds acquired was enough, however, to get living plants which turned out to be a new species, *Primula rupestris*, related to *P. sinensis*. Ere he died of a fever in Burma he found the sturdy *P. sonchifolia* which flowered in April and seemed to love forcing its way through the snow, the dainty, star-like *P. alsophila*, and the small rock-plant *P. moscophora*, which . . . "in sheeted masses twinkles at you as you climb the breakleg stairway". FARRER died in the jungles of Upper Burma. After his death they made a coffin and carried it on coolie-back to Konglu where he was buried in a clearing above the fort on Konglu-bum.

Out of Eastern Asia have come many of our finest members of the Lily family. They are distributed over the entire area between Afghanistan on the west, India on the south, Kamtschatka on the north and the Philippines on the east. In India, the lilies are generally found only high up in the mountains; in China they grow from sea level up to 13,000 feet; in Japan, Formosa and Korea they range from sea level to the high mountains while in their northern limits they are confined to low altitudes, usually river valleys. Probably the oldest and most widely cultivated is *L.*

tigrinum, the Tiger Lily. For more than 1000 years it has been grown by the Chinese for its bulb. Only in the foothills of the Lushan range does it grow wild in China, but it is plentiful in central Korea. The lily was formerly grown less for its flowers than for the edible bulbs. Species having white bulbs were preferred. But at present the lily is more widely cultivated as a garden flower.

European gardeners have depended upon oriental species of roses for breeding stock for many generations. LA QUINTINYE ("Instruction pour les jardins", 1697 edition) wrote of the Rose of China, but said it had several other names. He mentioned the size of the shrub, saying that it eventually attained the height of a tree. The parents of the modern cultivated rose of our gardens were three Chinese species. One of these, the China Monthly rose (*Rosa chinensis*), had been brought to India early in the seventeenth century by a captain of the British East India Company. It was introduced into Holland in 1781 under the name Bengal rose; hence it was thought to be a native of India. Sir JOSEPH BANKS brought it to England in 1789. In 1804 the first rambler rose (*R. multiflora,* var. *carnea*) reached England, followed in 1808 by the first tea-scented rose (*R. odorata*), both coming from China. These three species, then, have furnished the entire stock from which our modern roses have developed, hybridization and horticultural techniques having produced the wealth of garden forms now known.

The Hollanders appear to have had an outstanding passion for gardens and gardening. Their interest in exotic plants and the influence of the East brought home by traders further affected their garden designs. Holland was the plant nursery of Europe. From it emanated influences which spread to other lands. The Dutch doubtless first learned of the cultivation of oranges through the Italians, for in the middle of the seventeenth century Genoa was a great nursery for orange and lemon seeds. Needless to say, the climate of Holland would not permit the culture of citrus trees in the open, but the Dutch, in their enthusiasm, developed the orangery, which later became an important feature in the gardens of many other countries.

Acclimatization:- Little by little, as the introduction of foreign plants went on, gardeners and farmers learned that there was such a thing as adaptation to the new environment. This was empirically learned at first, but gradually came to be recognized as a characteristic of the living plant.

GUY DE LA BROSSE proposed to LOUIS XIII in 1628 a plan for a royal garden for the cultivation of medicinal plants, to which the sick might have recourse, where the students of medicine might learn, and where those who profess it might be addressed when needed. He reported that he had included not only domestic plants, but also those of the most distant countries which could be grown in the climate of Paris, not so much as to learn their appearance, as to try their virtues and to learn how they had changed their properties. BROSSE then relates some interesting things about changes. For example, said he:

"We know that many plants grown in a new region lose much of their original condition. The seeds of the Florentine sweet fennel are degenerate in

the third or fourth year, and cauliflower in the second. They report that the fruit of the peach is poison in Persia, but loses its "malice" when transplanted into Europe. However that may be, we do not wish to maintain that it is true of all. Tobacco (Peton) was cultivated for 50 years in France, and I know of no evidence that anyone has changed the seeds, yet it retains all the virtues which nature originally gave it. If it is not as potent as in its original home, at least it is proportional and is quite useful to us. The loss of properties is not as common as their decrease, because the seeds seem to transmit them."

PHILIP MILLER ("The Gardener's Kalendar", 1769) gave opinions which indicated that there had been progress in acclimatization and selection, saying that a number of exotic trees, shrubs, and plants which had been brought to Europe had then become:

> "as it were, denizens in England, being so far naturalised as to thrive in the open air without shelter . . . and by making trials with many of those plants which were formerly nursed up in greenhouses and treated with great tenderness, they have been found to thrive and flower much better when planted in full ground and treated with less delicacy."

One of PHILIP MILLER's first papers read before the Royal Society was "A Method of Raising Some Exotick Trees".

Sir HANS SLOANE, who will ever be remembered for his generosity to the Chelsea Physic Garden, wrote as follows in 1684 to RAY regarding their success in handling tender plants:

> "I was the other day at Chelsea and find that the artifices used by Mr. WATTS have been very effectual for the Preservation of his plants, insomuch that this severe winter has scarce killed any of his fine plants. One thing I much wonder to see. *Cedrus Montis Libani* . . . should thrive so well as without pot or greenhouse to be able to propagate itself by Layers this spring. Seeds sown last Autumn have as yet thriven very well."

A survey of the writings of the gardeners of that time affords evidence that this process of acclimatization, which started, of necessity more or less empirically, developed into one of the fine arts of gardening in the seventeenth and eighteenth centuries. The combination of the talents of men like PHILIP MILLER and Sir HANS SLOANE in acclimatizing non-indigenous plants enriched greatly the horticulture of England. MILLER's superb work entitled "Gardener's Dictionary" (1731) gave directions wherever possible for the selection of desirable characters in plants; *e.g.*, roguing the garden before seed formation, selecting seeds from early maturing plants, selecting seeds from the hardiest plants. In their time there was, however, a dependence of English gardeners upon Holland for satisfactory seeds. Whether the desired quality pertained to the vigor of the strain, early maturity, or freedom from disease was not stated. In many cases there was undoubtedly a lateness in maturity in England which prevented the plants from ripening their seeds. Therefore, it was necessary to look to some other country for fully matured seeds. MILLER's careful directions for the selection of seeds of flowering and kitchen plants were therefore important for the gardening industry.

WILLIAM WATTS (in a letter to the Royal Society in 1751) enumerated exotic trees he had observed in the gardens of the Bishop of London. The list included the black walnut, maple, cedar, and others from North America, the pistach, carob, Cedar of Lebanon, and others from the Near East. WATTS emphasized that

these trees grew successfully in climates and latitudes very different from their native habitats, and commented on the importance to the country of such introductions.

RICHARD BRADLEY's ingenious ideas about grafting exotics upon native plants to increase their hardiness were based on his observations that the grafted tree partook somewhat of the nature of the stock upon which it was worked. This original and valuable observation was subsequently applied with a certain amount of success to horticulture, but could not be applied to such extreme cases as BRADLEY suggested, *e.g.*, changing the species, or producing hybrid fruits by grafting one tree upon another of the same class.

In conclusion, emphasis must be laid upon the fact that men like BACON, LOCKE, CLIFFORD, BOERHAAVE, LA QUINTINYE, and PARKINSON were scientific gardeners in the sense that exact observations and experiments were included in their garden programs. If the modern garden, replete with plants of exquisite beauty and expressive of fine ideas, carries on the tradition of the ancient garden, no less do the university botanical gardens, the plant-breeding plots, the nurseries, the acclimatization gardens, and the agricultural experiment plots specialize in problems which intrigued the gardeners of a century long past, problems which they saw but were unable to solve.

REFERENCES:-

BRADLEY, RICHARD (1726): A general treatise of husbandry and gardening. 2 vols. J. Peele, London.

CECIL, EVELYN (1910): A history of gardening in England. Ed. 3 (with bibliography). Dutton, New York.

EVELYN, JOHN (1664): Kalendarium Hortense. Macock, London.

FALKENBERG, PAUL (1899): The garden and its development. Smithsonian Inst. Annual Report, 1899 (published 1901), Washington.

FARRER, REGINALD J. (1926): On the eaves of the world. 2 vols. E. Arnold, London.

GRAS, NORMAN S. B. (1940): A history of agriculture in Europe and America. Ed. 2, Crofts, New York.

GOLTZ, T. VON DER (1890): Geschichte der Landwirtschaft. *In his* Handbuch der gesamten Landwirtschaft 1:1-50. Laupp, Tübingen.

JOHNSON, GEORGE W. (1829): A history of English gardening. Baldwin & Cradock, London.

KNIGHT, THOS. ANDREW (1797): Treatise on the culture of the apple and pear. (several later editions). London.

LA QUINTINYE, JEAN DE (1699): The compleat gard'ner . . . (a translation by LONDON and WISE). Gillyflower, London.

MILLER, PHILIP (1731): The gardener's dictionary. (numerous later editions). Printed by the author, London.

PARKINSON, JOHN (1629): Paradisi in sole Paradisus terrestris. Lownes & Young, London. Also a facsimile reprint by Methuen & Co., London. 1904.

PULTENEY, RICHARD (1790): Historical and biographical sketches of the progress of botany in England . . . 2 vols. T. Cadell, London.

ROHDE, ELEANOUR S. (1924): The old English gardening books. Hopkinson, London.

TOLKOWSKY, SAMUEL (1938): Hesperides; a history of the culture and use of citrus fruits. Bale and Curnow, London.

WRIGHT, RICHARDSON (1934): The story of gardening. Dodd, Mead, New York.

Chapter IX.

PLANT GEOGRAPHY IN THE NINETEENTH CENTURY.

Pioneer works:- The world of plants and trees and its manifold relations with climate and continent began to be scientifically studied at the opening of the nineteenth century. Explorers had found plants and systematists had evolved ideas and schemes for their classification. There was then born of man's curiosity an impulse to know something about the physiognomy of the plants of mountain and plain, of island and continent. Specifically they asked "What are the relations between the *ensemble* of climatic factors and the character of the vegetation of a region like Europe or North America?" It is true that farmers and herdsmen had long possessed a certain empirical knowledge of the distribution of plants important for them and their flocks, but the great botanists had not previously thought of plants in terms of geographical distribution or migration.

One of the pioneers in the scientific study of plant geography was CARL LUDWIG WILLDENOW (1765-1812) of Berlin. He published a comprehensive study in 1792 entitled "Grundriss der Kraüterkunde zu Vorlesungen entworfen" (English translations appeared in 1805 and 1811).

It is doubtful whether anyone prior to WILLDENOW's time had given so good a description of the relation of seed dissemination to plant distribution or such clear concepts of plant associations. He commented on the characteristic limitations of species in a way which suggests faintly the idea of endemism, and also described the remarkable affinities often exhibited by plants of widely separated regions.

WILLDENOW observed that there was a remarkable resemblance between the trees and shrubs of northern Asia and northern America though there was slight resemblance between the herbaceous plants. Thus, he said, in northern Asia we find *Acer cappadocium, Alnus glutinosa, Fagus sylvatica, Sambucus nigra,* and the corresponding trees and shrubs in northern America are *Acer saccharinum, Alnus serrulata, Fagus latifolia,* and *Sambucus canadensis.* In like manner he commented on the similarities between the shrubs of the Cape of Good Hope and Australia, and likewise between the floras of the Bahama Islands and the neighboring continent.

Having formulated characteristics of the floristic areas of Europe, WILLDENOW sketched their centers of dispersal and their approximate boundaries. In so doing he remarked that they generally intermingle at the boundaries and enrich the flora of regions like southern France. He clearly recognized and tried to explain the dispersion of plants from definite centers, and the dependence

of plant geography on geological history. His was a veritable pathfinding piece of work.

The subject of plant geography received a great impetus from the writings of the traveller ALEXANDER VON HUMBOLDT (1769-1859), who likewise contributed to nearly every branch of science, and who was perhaps the last of the cosmographers. His conception of the universe as a whole was no less remarkable than his faculty of observing and explaining single phenomena.

In his native city of Berlin HUMBOLDT received a good education, and in the universities manifested unusual abilities. He was originally a student of geology and mining, but the desire for more freedom and especially for exploratory travel impelled him to resign his position with a mining syndicate and to prepare for travel. In Paris he met AIMÉ BONPLAND (1773-1858), a young French botanist, who joined him. They sailed from Coruña in June 1799 for Venezuela, where they explored prior to making their way to the Andes and Peru. Taking advantage of the exceptional opportunities of the country, HUMBOLDT devoted himself to studies on electrical and astronomical phenomena, but also acquired valuable information about the cinchona (quinine) tree and its culture. From Peru they went to Mexico where they explored for a year studying the physical geography of the country. They returned to France in 1804 and immediately proceeded to arrange their manuscripts and collections, a large part of which, however, had been lost by a shipwreck.

They published a work of 30 volumes "Voyage aux Régions équinoxiales . . ." of which the first 14 were devoted to botany; 5 were devoted to physical geography, geognosy, and astronomy; and 1 to the geography of plants.

HUMBOLDT seems to have observed, independently, that plants are grouped into societies, or associations; and speaks of the differing composition of plant associations in tropical and temperate zones. He showed the value of isothermal lines in physical geography and plant geography.

Among his minor works, "Ansichten der Natur" (1808) has had the widest distribution and has been translated into nearly every European language. In this book he gave short sketches of the life history of various plants and of the aspects of vegetation in the lands he visited.

Later in his life HUMBOLDT devoted himself to writing "Kosmos", an encyclopedic work in which he attempted a comprehensive explanation of the universe. This also was translated into many languages and made a profound impression.

The development of plant geography simultaneously received an added impetus from the work of ROBERT BROWN (1773-1858) a Scottish botanist of unusual talents. BROWN was appointed naturalist on the recommendation of Sir JOSEPH BANKS for a British expedition sent out under Captain FLINDERS for the survey of the Australian coasts. This gave him four years (1801-1805) for exploring the little known flora of that country. Soon after his return he was appointed librarian of the Linnean Society of London. His "Botany of Terra Australis" appeared in 1814. BROWN discerned that scarcely more than one tenth of the species found in "Terra Australis" had been observed in other parts of the world, and carefully compared them with other regions. He concluded

that the Australian flora resembled more closely those of India and South Africa than that of South America. BROWN was a man who could think of floras in terms of continents and could elaborate relationships which completely escaped others. A. VON HUMBOLDT called him *Botanicorum facile Princeps.* The papers he published on the affinities and geographical distribution of genera and species mapped out new fields in which much productive work was later to be done.

Formulation of concepts and terminology:- A further advance was marked by the publication of "Grundzüge einer allgemeinen Pflanzengeographie" by SCHOUW in 1823 in which important foundations were laid. The author, J. F. SCHOUW (1789-1852) was professor in Copenhagen and had been attracted to the study of plant geography by the works of HUMBOLDT. After a summer spent among the mountains of Norway and the years 1817-1819 in Italy and Sicily, he realized how little had been done toward establishing fundamental laws for the science of plant geography, and himself undertook to formulate the laws and establish the rudimentary principles for this new science.

We owe to SCHOUW several of the conceptions and much of the terminology which have since become fixed in the literature of plant geography. The first part of his book deals with the effect of external factors on the distribution of plants but, like other plant geographers of the time, he dealt principally with temperature. In addition, he was the first to give definite descriptions of certain societies and to recognize the grouping of plants according to the water content of the soil. The edaphic factors are fully outlined, but not explicitly treated. The effect of light is also very briefly treated: he dismisses it by saying, "Without doubt it also serves to nourish the plant".

SCHOUW looked for characteristic plants in the flora of each part of the world. He concluded that the genera *Solidago* and *Aster* were so predominant in North America that it could be denoted the kingdom of those genera. This kingdom was also characterized by oaks and pines and by a deficiency of *Cruciferae, Umbelliferae, Cichorieae,* and *Cynareae,* an absence of Heathers and an excess of *Vacciniaceae.* So also, the kingdom of the *Magnoliae* was characteristic of the most southern parts of the United States. He said, likewise, that the flora of southern Europe is the kingdom of the *Labiatae* and *Caryophyllaceae,* since the region is the habitat of so great a number of species of those families. He was thus doing in a broader and more comprehensive way what THEOPHRASTUS had done in his time.

In the dawn it was hard to distinguish the essential features of this unexplored field of botany. When it came to understanding the distribution of plants of remote and isolated regions, botanists were confronted with a hard problem.

The comparative readiness with which air temperatures can be determined and isothermal lines established afforded a method extensively utilized in mapping life zones. In spite of a certain amount of naïveté on the part of the earlier workers, among whom MEYEN may be noticed, the general boundaries of life zones were established. MEYEN (1804-1840) discerned the similarity of alpine plants of distant mountain ranges, but was baffled by the absence

of vegetative bridges between them. His ingenious, but specious, theory of Spontaneous Generation (1836) was the only escape possible to him. Shackled as they were by the theory of the constancy of species, botanists of that day gave attention principally to discussions of the validity of species descriptions. Rather than admit that there had been any change in life forms they cried that the species had been founded on inconstant characters, and that what is inconstant cannot define the species!

J. Thurmann, in "Essai de phytostatique" (1849) elaborated on the importance of the subjacent rocks on the distribution of plants in the Jura. Hard rocks are sterile on account of their unchangeability which is opposed to the formation of detritus. Soft rocks are sterile occasionally in consequence of their compactness and impermeability.

The subject of plant geography was greatly clarified and methods of attack were formulated by Alphonse de Candolle (1806-1893) who had a particular aptitude for numerical and exact forms combined with an acquaintance with the physical sciences. He inherited the industry and ability of his father, Augustin Pyrame de Candolle (1778-1841). His book "Géographie Botanique Raisonnée" was published in 1855.

De Candolle tried to discover the laws of the distribution of plants on the earth. He devoted considerable space to the role of temperature in geographic distribution. He distinguished between the temperatures effective for plant growth and those which (being near or below the freezing point) are sub-minimal for growth. He concluded that the summation of temperatures effective for growth was a useful criterion for determining the range of species. At the cost of great labor he computed temperatures within the range and near its limits for many species, and the areas of species according to families. Darwin commended de Candolle's discussion of the relation of the size of families to the average range of individual species, but believed that a better method would have been to use the size of genera instead of families as a basis. The problem of the origin of existing species was considered and he concluded that there are numerous facts which go far to prove the geological antiquity of the greater part of existing species; and that their creation was probably successive.

Floristics:- The classical studies of Joseph D. Hooker (1817-1911) on geographical distribution, endemism, and affinities brought to a climax the investigations of the mid-nineteenth century botanists. He was the second son of Sir William Jackson Hooker (1785-1865) professor of botany in Glasgow and, subsequently, director of Kew botanical garden. In 1839 at the age of 22, Joseph, having passed his examinations in medicine, enrolled as assistant surgeon and botanist on the "Erebus" then about to start in company with the "Terror" on a trip lasting four years under command of Sir James Ross. The purpose of the trip was a magnetic survey of the Antarctic region, giving Hooker an opportunity to collect and observe in many places in the southern hemisphere. When the season prevented the ship from entering the circumpolar seas they visited islands and continents where Hooker had opportunities to make botanical studies.

The results of his botanical work were assembled and published (1844) in "Flora Antarctica", an epoch-making publication in the realm of floristics. It contains not merely reports of explorations, or descriptions of new species, but illuminating discussions of distribution, which were the most scientific essays up to their time. In them he commented on the uniformity of the flora of the Antarctic islands and on the similarity of species on the high mountains of southern Chili, Australia, Tasmania, and New Zealand. The work was highly esteemed by LYELL and DARWIN. The latter wrote, "I have finished your essay. To my judgment it is by far the grandest and most interesting essay on subjects of the nature discussed I have ever read". HOOKER travelled widely in studying plants. His enthusiasm for the field led him to make arduous journeys to observe and to collect plants in distant countries. In 1848

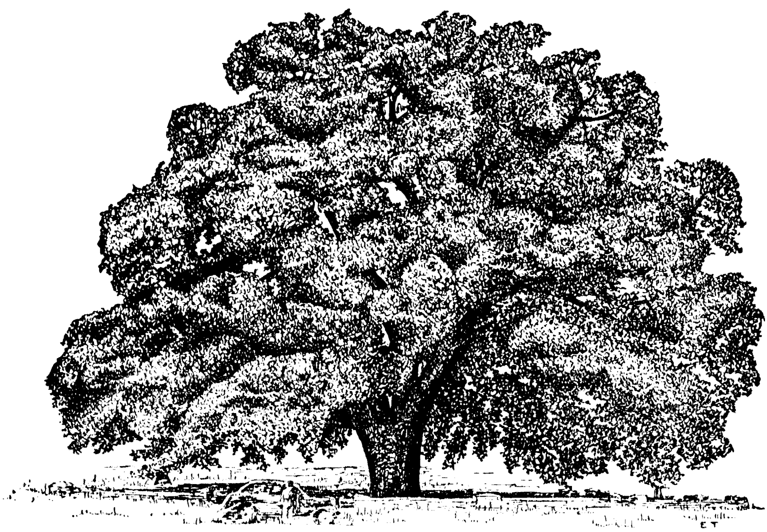


FIG. 21. — The Hooker Oak at Chico, California, a large specimen of *Quercus lobata*, dedicated to Sir JOSEPH D. HOOKER, who visited California in 1877 with Dr. GRAY. Drawn from a photograph taken in 1938. Height of tree 101 feet. Allowing two square feet for each person, 7,885 people could stand under its branches.

he went to India where he remained for three years obtaining results which provided material for much of his later writing. In 1860 he joined an expedition to Syria and Palestine; in 1871 he made the first botanical exploration of the Atlas range, and in 1877 visited the western United States in company with ASA GRAY.

From first to last HOOKER was interested primarily in geographical distribution, and he successfully elucidated the important subject of endemism. What he did for the Antarctic flora in his youth he continued in mature life for the Indian flora. The "Flora of British India" (1872-1897) was, as he said, a pioneer work, but he expressed the hope that it might "Help the phytogeographer to discuss the problems of distribution of plants from the point of view of what is perhaps the richest, and is certainly the most varied botanical area on the surface of the globe". HOOKER was not only a scientific systematist, he was interested in the great

question of the origin of species and an intimate counsellor of DARWIN. His conclusions on the evolutionary question were based on his intimate studies of life forms in many parts of the world.

AUGUST GRISEBACH (1814-1879) was one of the first to define types of physiognomy of vegetation with respect to climate. In "Die Vegetation der Erde" (1872) he named and accurately described 54 (eventually 60) vegetative forms, arranged according to the important climatic regions. In this he emphasized and elaborated ideas first proposed by HUMBOLDT, but his work was a great advance upon all that had been done previously, and had a very significant influence upon all subsequent work in plant geography. GRISEBACH travelled widely. He was appointed professor of botany at Göttingen in 1841 and director of the botanical garden in 1875.

GRISEBACH seems to have comprehended fully the implication of evolutionary concepts in interpreting floristic characters. He

FIG. 22. — The Gray Herbarium of Harvard University, an important center for botanical work. The depository of many collections of plants. GRAY resided in the house at the left. (From a picture made about 1890).

was aware that the mutability of organisms and their powers of response to their habitats were factors of great importance for understanding the problems of physiognomy. It is not surprising to find several references to GRISEBACH's work in DARWIN's letters.

The problems of floristic plant geography in North America were elucidated by the work of ASA GRAY (1810-1888) of Harvard University. His extensive study of the vegetation based on material sent by various explorers in the western part of the continent and obtained on his own travels, developed a comprehensive conception of the varied plant formations of the United States.

In an address delivered in 1884 he surveyed the characteristics of the North American flora in a way that has been unexcelled. The origins of the flora were succinctly discussed and its affinities with other continental floras were depicted.

One of his most important works was on the affinities between the floras of Japan and North America (1859). Important because it discussed the question whether the observed distribution of congeneric or other nearly related species is primordial, and therefore beyond all scientific explanation, or whether it may be to a certain extent a natural result. In it we find the method and spirit of DARWIN exemplified. It opened the road for the introduction of the new ideas on the origin and relationships of living things and showed that GRAY could make excursions into the realm of ideas as well as that of plants.

Other writings of GRAY's dealt with Forest Geography and Archaeology in which questions of endemism and rainfall were discussed. "Sequoia and its History" was written in 1872.

The epoch-making work of A. ENGLER (1844-1930), "Versuch einer Entwicklungsgeschichte der Pflanzenwelt" (1879-1882), is certainly one of the outstanding works on floristic plant geography. He was appointed professor of botany and director of the botanical garden in Berlin in 1889. His comprehensive studies were summarized in 36 theses and presented in an introductory chapter. ENGLER was also impressed with the importance of the geological history for the understanding of floristic problems. Time and again he went back to the tertiary epoch in correlating the plant distributions. He has been criticized for his emphasis on the effects of the Ice Age and other geological epochs on contemporaneous vegetation, but his exposition of the importance of the geological history cannot be gainsaid.

The floristic aspects of plant geography were further elaborated by OSCAR DRUDE (1852-1933) in his "Handbuch der Pflanzengeographie" (1890). The development of floras was considered primarily with respect to the physical geography of the land area, with proper recognition of climatic factors and is strongly reminiscent of the concepts of GRISEBACH. He grouped the vegetation of the earth into 20 floral kingdoms, and in his later works into 35 groups.

DARWIN's "Origin of Species" gave a great stimulus to the study of all biological phenomena, but especially to that of adaptation. Of all the books which preceded, it dealt most directly and scientifically with the origin and meaning of adaptation. It is not too much to say that DARWIN excelled all others who had attempted to explain the problems of adaptation since the struggle for existence selects the organisms which possess adaptations fitting them to their environment.

Following his first great work came further studies on adaptations of plants - Insectivorous Plants, Climbing Plants, The Power of Movement in Plants, Animals and Plants Under Domestication, etc.

Physiological plant geography:- The growing appreciation of the importance of the physiological factors in plant geography came to fruition in the last quarter of the nineteenth century. It became increasingly clear that there were intimate relations between the plant and its environment which should be investigated on a physiological as well as a floristic basis. Investigations in this field deal with the economy of plants and their responses to environmental conditions.

This province has been variously designated as Oecological Plant Geography, Physiological Plant Geography, or Ecology. He who can visualize the plant as an integration of living parts, or the meadow as an integration of individuals and species, has embarked on the study of ecological botany in its broad sense. The problem of the influence of environment on the plant which had been started by HUMBOLDT was seriously undertaken by VESQUE in 1878 and by BONNIER and FLAHAULT (1879). The last named men explored the peninsula of Scandinavia and compared its flora with that of the Alps. They discovered many important relationships between the plant forms and soil-light-heat conditions. BONNIER's experimental cultures extended the previous knowledge of the effects of climate on plant forms and FLAHAULT developed new methods of research in Plant Sociology.

VOLKEN's work on the flora of the Egyptian-Arabian deserts (1887), while descriptive, was a great demonstration of the importance of ecological methods in plant geography.

SCHENCK turned especial attention to the relations of aquatic plants to their environment (1886). Leaving to his colleagues the task of travelling to distant lands, he took up a careful biological study of the plants near at hand. He investigated such subjects as the anatomy of the submerged organs, the wintering of the plants, the germination of the seeds, etc. SCHENCK showed the immense value of such work for the study of adaptations.

The problems and results of this province of plant geography were formulated and discussed (1895) in "Plantesamfund" (Ecology of Plants) by EUGENE WARMING (1841-1924), professor in Copenhagen. The appearance of the book was timely and it had a great influence on the subsequent development of ecology.

WARMING discussed anew the factors of the environment and developed new ideas on adaptations of plant formations. One by one he studied and described the plant formations with respect to the physico-chemical factors of their habitat. He concluded that every species must be in harmony, as regards both its external and internal construction, with the natural conditions under which it lives. It will be exterminated or displaced by other species, when the change in the environment is so great that adaptation is impossible. "Thus", said he, "we impinge upon the problem of the origin of different species".

A. F. W. SCHIMPER (1856-1901) shortly thereafter published "Pflanzengeographie auf physiologischer Grundlage" (1898). This scholarly and important work showed what had been done toward a complete study of the plants of the world and included results of his own studies. His genius for exact observation and his ability to systematize knowledge would have delighted HUMBOLDT. In the book SCHIMPER discussed (a) the environmental factors, (b) formations and guilds of plants, and (c) zones and plant geographic regions. He considered that the relations between the forms of plants and the environmental conditions at different places on the earth's surface were the legitimate province of physiological plant geography. From first to last he connected the morphology and physiology of plants with their grouping into zones and regions.

The earlier idea of the biological unity of natural plant associations began to be elaborated in the latter part of the nineteenth century. STEBLER and SCHROETER investigated (1892) the plant

associations of the Alpine meadows and pastures, concluding that these natural associations had a biological unity. As expressed later by FLAHAULT and SCHROETER, "An association is a community of certain floristic composition, of uniform habitat conditions, and of uniform physiognomy". Under the hand of SCHROETER and his disciples the ideas of plant sociology have been more fully developed, as shown in several modern books. POUND and CLEMENTS' description of the phytogeography of Nebraska was the first of a series of studies which have been extensively developed in America. The idea of Succession of plants has been promulgated by CLEMENTS and by COWLES in America.

The twentieth century has been a time of rapid development for ecological plant geography and has seen precise methods of investigation supplant some of the hasty reconnaissant methods of earlier days. Gradually the weaknesses which characterized some of the observational type of work are being eliminated as systematists, physiologists, and geneticists are combining to study the great problems of the vegetation of the earth.

REFERENCES:

BONNIER, G. E. M. and FLAHAULT, C. (1879): Observations sur les modifications des végétaux suivant les conditions physiques du milieu. Martinet, Paris.

BRAUN-BLANQUET, J. (1928): Pflanzensoziologie. Springer, Berlin.

—— —— (1932): Plant sociology; transl. by FULLER and CONARD. McGraw-Hill, New York and London.

BROWN, ROBERT (1814): General remarks, geographical and systematical, on the botany of Terra Australis. Appendix to: FLINDERS, M., Voyage to Terra Australis. London.

CANDOLLE, A. L. P. P. DE (1855): Géographie botanique raisonnée. Masson, Paris.

FLAHAULT, C. (1881): Nouvelles observations sur les modifications des végétaux suivant les conditions physiques du milieu. Paris.

—— —— (1907): Les progrès de la géographie botanique depuis 1884. Proggressus rei botanicae, I:243-317.

GRAY, A. (1889): Scientific papers . . . selected by C. S. SARGENT. Houghton Mifflin, Boston and New York.

HUMBOLDT, A. VON (1807): Essai sur la géographie des plantes (*In* HUMBOLDT, A. VON, & BONPLAND, A.: Voyage, part 5, Physique générale et géologie. F. Shoell, Paris).

—— —— (1850): Views of nature . . .; transl. from the German by E. C. OTTÉ and H. G. BOHN. Bohn, London.

REED, H. S. (1905): A brief history of ecological work in botany. Plant World 8:163-170, 198-208.

SCHIMPER, A. F. W. (1898): Pflanzengeographie auf physiologischer Grundlage. Fischer, Jena.

—— —— (1903): Eng. transl. by W. R. FISHER. Clarendon Press, Oxford.

SCHOUW, J. F. (1822): Grundtraek til en almindelig Plantegeographie. Gyldendal, Kjøbenhavn.

—— —— (1823): (German translation) Grundzüge einer allgemeinen Pflanzengeographie. Berlin.

WARMING, E. (1895): Plantesamfund. P. G. Philipsen, Kjøbenhavn.

—— —— (1909): Oecology of plants (Eng. transl. by GROOM and BALFOUR). Clarendon Press, Oxford.

Chapter X.

MORPHOLOGY.

The first hundred years—from Linnaeus to Hofmeister:- The science of botany was dominated at the beginning of the 19th century by the achievements of systematists who had made such notable progress in the preceding century. Although LINNAEUS had written "Philosophia Botanica" it probably does not justify the title. His ideas on morphology seem superficial, since they were elaborated for the practical purpose of classifying plants and were often dominated by a spirit of scholasticism. He propounded the theory that one form grows out of another, *e.g.*, he derived leaves and parts of flowers from parts of the stem, and considered (as many a subsequent student has done) that the parts of flowers are modified leaves.

Although CASPAR FRIEDRICH WOLFF had made (1759) a valiant beginning by his study of the development of organs from the growing point, the subject of developmental morphology received its greatest impetus from one to whom WOLFF's work was unknown. This man was the Poet-Philosopher GOETHE (1749-1832), founder of a school of idealistic philosophy in botany, whose writings though entertaining, were often a puzzling combination of shrewd observation and *a priori* reasoning. GOETHE gave his doctrine the caption "metamorphosis", but the word as employed in botany has not the same connotation as in zoology, because the embryo of the plant develops along lines entirely different from the embryo of animals.

GOETHE said (Doctrine of metamorphosis, 1790): "It is open to observation that certain exterior parts of the plants sometimes change and pass into the form of adjacent parts, either wholly, or in a greater or less degree". He formulated the concepts of a normal (ascending) metamorphosis and an abnormal (descending) metamorphosis. A foliage leaf might expand into a sepal in normal metamorphosis, or contract into a stamen in abnormal metamorphosis. Everything in plant forms was idealized.

GOETHE unfortunately used the term metamorphosis at one time literally and at another time figuratively, leaving one to make his own interpretations. At this distance it is unprofitable to attempt to clarify his confused and, at times, contradictory views. GOETHE and his followers derived an idea of archetypes from PLATO, according to which every plant has a fundamental plan, if only one could discover it. GOETHE was more indefinite about a spiral, ascending metamorphosis by which the parts of a plant underwent cyclic transformation. His idea that the cyclic tendency in plants represents the female, and the vertical tendency the male, exemplified the extreme of idealistic philosophy. Although much of what he wrote on this subject seems strange to us today, out of it came the valuable idea that the stuff of life is plastic and that there is the possibility of change.

The idealistic interpretation of morphology was subsequently propagated enthusiastically by men who were, in spite of certain aberrations, imbued with the principles of scientific research. K. F. SCHIMPER (1803-1867) made a serious attempt to learn something about the spiral arrangement of leaves by a system of numerology, which anyone with good eyesight and a little patience could use. He found that the divergences of leaves on the stem can be reduced to a few types expressed by the series of fractions 1/2, 2/3, 3/5, 5/8, 8/13 etc. The whole thing had a deceptive simplicity, but it enabled the observers to make concise and elegant descriptions of the intricacies of leaf arrangement. Although the business of leaf counting and number writing in themselves were fruitless exercises, the ideas of phyllotaxy advanced the study of morphology by demonstrating that organs had a definite distribution in space.

ALEXANDER BRAUN (1805-1877), a leading and influential German botanist, sought to discover the principles of growth and form in the processes of regeneration and rejuvenescence. Although he contributed to the advancement of morphology, he retained many idealistic concepts of plants. BRAUN made an important distinction between stem, leaf, and root in contrast to GOETHE's idea of the archetype. The stem, with its leaves, was one unit of structure and the root another. Furthermore, he maintained (perhaps for the first time) that the succession and alternation of shoots in the development of the plant represent facts of importance for morphology. In the development of the shoot (or bud) a succession of leaf metamorphoses may be observed, namely, "cataphyllary", "euphyllary", "hypsophyllary", "sepals", "petals", "stamens", and "pistils". In BRAUN's mind these successive leaf formations represent a striving for completeness, a process which begins anew with each shoot. His belief in the essential homology of all the structures of his seven formations was an outgrowth of his idealistic philosophy of plants.

Before the ideas of the school of idealistic botany had run their course, a strong counter movement had been started by SCHLEIDEN (1804-1881) who insisted that botany is an inductive science. He examined and criticized with asperity the ideas of all his contemporaries. Iconoclastic to an extreme, he advocated the disregard of most works that had been written prior to the appearance of his "Grundzüge". Quoth he,

> Books have been written when plants should have been examined, conjectures have been made when investigations should have been pursued. Hence for about a century we have but revolved in a circle, without making the least advance or discovering new facts . . .

Happily these scathing criticisms stimulated men to new, objective researches on plants. It was the period when the importance of developmental morphology was recognized. In spite of a certain amount of incompleteness, SCHLEIDEN's "Grundzüge der wissenschaftlichen Botanik" (1843) is a remarkable book, one which will still repay studious attention.

A. P. DE CANDOLLE (1778-1841) labored to establish theoretically the unity which lies at the basis of the most diverse plant configurations. He thought that the most diverse genera of each

family, as well as the families could be referred to a definitely regular and systematic "type". The German school under JUNG and GOETHE had sought this unity in the several parts of the same plant; the French school under JUSSIEU and ADANSON had sought the same unity for the analogous parts of different groups of the plant kingdom. DE CANDOLLE apprehended that both types of endeavor should be unified, but he erred when he thought that he had actually succeeded in uniting them so that "Each might serve for the fulfillment of the other". He spoke always of organs, designating the cells as "elemental organs", the stems, roots, and leaves as "fundamental organs"; yet he said little of the relationships into which his theory brought all plants or organs.

Following the work of these pioneers in the field of morphology there was a more scientific, objective study of what we now recognize as fundamental morphology. Its progress was so closely related to a series of fundamental studies on the lower and higher plants that we must give consideration to the discoveries about the morphology and anatomy of thallophytes and bryophytes before proceeding to discuss the larger problems.

The formation of the assemblage called thallophyta was made in 1836 by ENDLICHER (1805-1849) who based his classification on the absence of organs which could be considered stems and leaves. While it is not quite true to say that some of the kelps like *Laminaria* lack stems and leaves, yet in view of their habits and methods of reproduction, the classification is now generally recognized. Whatever the form of the vegetative bodies their sex organs are one-celled, or, if multicellular, the gametes are not surrounded by a layer of sterile cells.

Although VAUCHER (1763-1841) discovered (1803), conjugation in some algae it was not until 1857 that PRINGSHEIM discovered the process of fertilization in *Saprolegnia* contributing thereby to the understanding of developmental morphology in the lower orders of plants. In chapter 17 it will be shown how TULASNE, OERSTED, PRINGSHEIM, and DE BARY demonstrated the cycles of development in the fungi and explained the nature of the asexual and sexual generations.

The belated development of the knowledge of the comparative morphology of the thallophytes possibly accounts for the absence of such weird and occult ideas as attended the morphology of the flowering plants.

The antheridia of mosses were seen by HEDWIG (1730-1799) and NEES VON ESENBECK (1776-1858) observed (1822) the discharge of the antherozoids of *Sphagnum*. UNGER (1800-1870) discovered (1834) the antherozoids of this plant and rightly assumed their function. MIRBEL (1776-1854) described in a classical treatise the remarkable structure of *Marchantia*, the development of gemmae, germination of spores and was the first to show the adaptability of bryophytes for experimental morphological investigations. He saw the egg-cell of the archegonium, but did not realize its significance. VALENTINE is generally credited with the discovery of the egg-cell of the archegonium, but his ideas of the sexuality of mosses were inferior to those of HEDWIG. He determined the position of the archegonium but did not recognize how the sporophyte grew out of it. ROBERT BROWN (1773-1858) had early been attracted to the study of mosses but the true nature

of fertilization in the group was not understood at the time. He considered the spores as seeds, reflecting the ideas of his time that the structures must be homologous with those of flowering plants. SCHLEIDEN failed to grasp the meaning of these organs and declared dogmatically that mosses, club-mosses, ferns and horse-tails are sexless. He regarded most of what had been said about antheridia and antherozoids as imagination.

The alternation of generations in plants:- A new, vivifying spirit came into plant morphology when WILHELM HOFMEISTER (1824-1877) published his "Vergleichende Untersuchungen" (1851) in which the comparative morphology of the higher cryptogams was elucidated.

HOFMEISTER's achievements are the more remarkable since he never attended a Hochschule or University. The son of a music-dealer and a music-dealer and bookseller himself, he was called at the age of 39 to a Professor's post in Heidelberg whence he went in 1872 to Tübingen. His most productive period in research was that during which he was engaged in business, but he trained, while in Heidelberg, some of the eminent botanists of the later 19th century. From Heidelberg he issued his two chief books, "Lehre von der Pflanzenzelle" (1867) and "Allgemeine Morphologie" (1868).

HOFMEISTER recognized the "corpusculum" of ROBERT BROWN as an archegonium, and the endosperm on which the corpuscula are formed as the prothallium which, however, was formed in the interior of the macrospore and no longer lived independently. He was the first to demonstrate that the moss plant corresponds to the prothallium of the vascular cryptogams and to the endosperm in the conifers. He greatly clarified the ideas on the morphology of bryophytes by his investigations on *Anthoceros*. His distinction between the vegetative structure and the sexual organs it produces was something new and timely. He finally demonstrated the process of sexual reproduction in the bryophytes which had been regarded by many botanists as "agamic" plants.

The crowning achievement was HOFMEISTER's establishment of the alternation of generations in the plant kingdom. Starting with the more obvious cases of the mosses and ferns, he extended the relationship of gametophyte and sporophyte generations to the gymnosperms and angiosperms. We owe much to HOFMEISTER's skill and patient observation by which the facts were discovered, but it is not amiss to say that he left it for later writers to discuss and to champion the law of the alternation of generations.

The antheridia of fern prothalli were discovered independently by NÄGELI in 1844 although he apparently did not recognize at the time the importance of his discovery. He failed to recognize the archegonia for the female sexual organs. A short time thereafter Count LESZCYC-SUMINSKI discovered (1847) archegonia but considered them as naked ovules from which embryos developed. This discovery aroused great interest and really marked an advance. He described the antheridia and antherozoids, detecting the tufted cilia which NÄGELI had overlooked. He described the archegonia incorrectly as ovules without envelopes consisting of a papilla (the neck) which, when perforated, gave the antherozoid access to the embryo sac within. He was correct, however, in

tracing the further development of the embryo and its various organs. He thus clearly showed sexuality in ferns since the sexual organs are produced on the prothallus and the embryo plant is the result of a process of fertilization.

The discovery of sexual organs in other pteridophytes followed shortly. HOFMEISTER succeeded (1852) in germinating spores of *Equisetum* and in producing prothallia bearing antheridia and archegonia. He presented (1855-57) the first complete account of the life history of *Isoetes* although many puzzling questions were left for later botanists to answer. He apprehended the importance of the pteridophytes as links between the old group of cryptogams and the phanerogams. Furthermore, his researches inspired great activity on the part of others in the study of the entire field of comparative morphology.

FARLOW (1844-1919) added a significant fact when he discovered (1874) that in certain ferns the sporophyte might arise vegetatively from the gametophyte without the formation of archegonia, a phenomenon he called "apogamy".

PRINGSHEIM (1824-1894) discovered the corresponding phenomenon, "apospory", in mosses in 1877. He thereupon formulated the theory that the gametophyte and sporophyte generations in the mosses were homologous and that sporangia were likewise homologous with antheridia and archegonia. He postulated a fundamental agreement between the somewhat irregular alternation in algae and fungi and the regular alternation of generations in mosses and pteridophytes. The alternation in mosses is thus due to the reduction of the indeterminate series of asexual forms of the thallophytes to one which remains inseparably connected with the sexual generation on which it originates. Refusing to split hairs about the relations of thallophytes to the higher plants, he carried the concept of homology upward and extended it to the gametophytes and sporophytes of the highest as well as the lowest forms of plants.

CELAKOWSKÝ (1834-1902) agreed in many particulars with PRINGSHEIM's concepts, but introduced the view that the sporophyte of the moss is not only antithetic to the gametophyte in completing the life cycle, but is a third type of generation interpolated between the sexual and the first neutral or asexual generations of the thallophyte.

In the next few years there was lively discussion of the origin of the sporophyte and the trend of its evolution in the higher vascular plants and whether it has passed through a stage analogous to the sporogonium of mosses and liverworts.

Eventually the problem was clarified by BOWER (*b.* 1855) who supplied (1890) evidence in the support of CELAKOWSKÝ's idea. The intercalated sporophyte, said he, has been produced by the amplification of the zygote. The subdivision of the zygote into numerous cells has brought about, as the result of a single sexual fusion, the possibility of a large number of offspring. In the lower forms the sporophyte is all sporogenous, but, as its size increased, a progressive sterilization of its tissues ensued, leaving only a part which possessed the function of spore production. Moreover, this progressive sterilization in the pteridophytes may account for many stages in their evolution. BOWER concluded that there was no evidence of a sporophyte in the algae, though the

archegoniate plants undoubtedly rose from the algae. The access to water was an occasional occurrence when certain forms acquired a terrestial mode of life, thus less dependence could be placed on sexuality for reproduction and an alternative method of increase of individuals was substituted. The zygote when once fertilized might then divide up into portions which could originate new individuals and the absence of water would favor their dispersal. In forms which acquired a habitat on land, the sporophyte assumed a higher morphological and physiological differentiation in which the acquisition of a food supply was highly important. In a later modification of his views, BOWER concluded that the alternation of generations in the archegoniates should be discussed on its own merits and not as a homologue of algae and fungi which are not subject, as he said, to "amphibial stabilization". BOWER's introduction of the biological concept into the theory of alternation of generations threw a new light on the problem. He emphasized and verified an earlier view that vegetative advance in the evolution of plants is conditioned on the sterilization of potentially propagative cells.

Support for the antithetic view of the sporophyte was advanced in 1894 by STRASBURGER and others who discovered that the number of chromosomes was reduced in the divisions of the spore-mother cells. STRASBURGER considered that the reduction-division may be interpreted as a return to the original condition, from which, after it has attained sexual differentiation, offspring are produced having a double (diploid) number of chromosomes.

Opposition to the antithetic view was raised by those who maintained that the origin of the sporophyte of terrestial plants was the differentiation of a vegetative form, fundamental to gametophyte and sporophyte alike. The latter view was championed (1896) by SCOTT (1854-1934) who emphasized that the zoospores formed from the germinating oospore are in no way different from the so-called zoogonidia formed on the vegetative plant at various stages of its growth.

The upshot of all the investigations was the establishment on a sound basis of the fact of an alternation of generations throughout the vegetable kingdom. The long task was finally completed 80 years after HOFMEISTER started his independent, epoch-making work. There are some wide gaps between the morphology of the algae and the archegoniates but they do not controvert the concept of alternation of generations. Nevertheless, it must be realized that the controversy between the adherents of the "homologous" and "antithetic" theories of alternation is by no means settled. Important evidence has been recently obtained from a study of existing as well as extinct plants which at present precludes summary judgments.

The stele:- The importance of the central cylinder of the stem was realized long before any success crowned the efforts of those who attempted to classify its tissues. DE CANDOLLE distinguished (1819) cortex, liber, alburnum, lignum, and medulla as the components of woody stems, but had no genuine comprehension of the organization of the stem. There was no real insight into the problem of histology at that time, in fact, one may say that the problem was then in the condition where it was left by MALPIGHI

and GREW. DE CANDOLLE classified stems of the higher plants as exo- and endogens upon the basis of the differentiation of the stem tissues. The earlier writers found this classification useful and adopted it. CARL SANIO (1832-1891) started the investigations which led to the understanding of secondary meristems, the origin and structure of secondary tissues, etc. He emphasized continually the ontogenetic features of the growth of tissues. He discovered (1863), not only the place and method of origin of the cambium, but also its cyclic activity and the consequent formation of annual rings of wood. Men had known in a vague way something about secondary growth of woody plants since the time of DUHAMEL, but SANIO brought to it precision and clarity.

DE BARY's encyclopedic work on comparative anatomy appeared in 1877 and represented, in the author's words, "an epitome of the present knowledge of the anatomy of the vegetative organs of vascular plants". This scholarly compilation emphasized the anatomy of the matured tissues of the plants and deliberately minimized the ontogenetic aspects of anatomical problems. DE BARY's viewpoint was based upon the conviction that the mature structure of the plant required more careful attention than juvenile stages which, in his opinion, had been overemphasized by many workers at that period.

The theory of the stele was formulated by VAN TIEGHEM (1839-1914) which is fundamental to much subsequent work. He concluded that root and stem are essentially similar since each possesses a stele (a definite central core) and a cortex which surrounds the stele. In the stem the stele may not be as distinct as in the root, in both organs the stele contains "conjunctive tissues" as well as vascular strands. He defined the pericycle as the limiting layer of the stele, the endodermis as the inner layer of the cortex, and the epidermis as its outer layer. He emphasized the fact that roots have a symmetrical structure, not only with respect to their vascular bundles, but with respect to the arrangement of secondary roots. VAN TIEGHEM and his students elaborated his theory, on the basis of comparative morphology and phylogeny. Although they laid a solid foundation for the further study of this important structure, they were unsuccessful in showing that all stelar types might have arisen from a single type.

SACHS concluded that the origin of the cambium ring was the chief difference between roots and shoots in the gymnosperms and dicotyledons. The difference, said he:

> Consists merely in the fact that in roots the phloem does not lie outside the xylem bundles (in the radial direction), but is disposed alternately with it on the periphery of the axial fibrovascular cylinder. When the cambium is once formed, it behaves in precisely the same manner as it does in the stem.

JEFFREY (*b.* 1866) who modified VAN TIEGHEM's concepts of the stele, introduced the terms siphonostele and protostele, the former being tubular, and the latter rod-shaped. He concluded that the siphonostele had arisen from the protostele, hence there is actually a basic (phylogenetic) homology between the two types.

JEFFREY's work convinced him that the pith is extrastelar in origin, and that it represents cortical tissue which invaded the stele in its phylogenetic evolution. Not only did the cortex thus

invade the stele, but phloem, pericycle, and endodermis also entered the xylem core. Thus he accounted for the primitive type of siphonostele which possesses internal phloem, pericycle, and endodermis. As evolution of plant structures proceeded these extrastelar tissues tended to disappear leaving only a perimedullary zone to represent the morphological history of the stele.

There has been a great amount of controversy and discussion of the anatomy of the stele, but it cannot be summarized here. There can be little doubt but that the evolution of the stele has been a significant factor in the development of ferns and their allies. The importance of the vascular system can only be appreciated when one considers the long process of progressive adaptation to terrestial life and the dominant position of gymnosperms and angiosperms in the vegetation of the earth. TANSLEY referred some of the anomalous structures in the stele of the ferns to the blind alleys into which the evolutionary processes wandered.

One who surveys the voluminous literature on the stele is inclined to marvel at the great amount of controversy and discussion about its structural anatomy. We will do well, therefore, to recall the words of BOWER:

> A conducting column constructed as is that of a Dicotyledon or of a gymnosperm is thus a living whole: as such it suffices for meeting the requirements of *unlimited* growth. The adjustment of extending efficiency to increasing requirement is *automatic*, whether it be in respect of mechanical strength, of storage space for formative material, or of capacity for water-transit: while ventilation is provided for by the intercellular spaces which traverse the medullary rays. The method of increase by cambial activity is such as will meet each of these needs until the limit of mechanical resistance is reached. Beyond this some change of material, or of the method of its use would be necessary to prevent collapse. (Size and form in plants, 1930).

Systematic Organography:- The idea that a plant has an orderly arrangement of its parts had been expressed in various ways by the botanists of the 18th and earlier centuries. The systematists had made general use of the concept in constructing their schemes of classification, but the idea of organography was still vague in the minds of most botanists at the beginning of the 19th century.

Inspired by the idea of a natural system for the classification of plants, A. P. DE CANDOLLE (1778-1841) proceeded to formulate (1813) an idea of symmetry in the structure of plants. We see in his efforts the beginning of an earnest attempt to use comparative morphology, not as an end in itself, but as the means to an end. He was at that time formulating his ideas on classification which he believed would be based on the plan of symmetry, especially of the floral organs. DE CANDOLLE's concepts were an expression of the belief that there is some sort of unity in nature, though he did not lose himself in the fantastic numerology of some of the nature-philosophers of that time. His doctrine of symmetry was the basis of all systematic morphological work in France for many years. Unfortunately he and his followers concerned themselves too exclusively with the morphology of the mature plant, neglecting developmental morphology.

The importance of anatomical characters in organography was emphasized in 1872 by VAN TIEGHEM (mentioned in a previous paragraph). The three fundamental organs he distinguished were

roots, stems, and leaves. The root is characterized by its axial symmetry and by the centripetal differentiation of its primary woody bundles; the stem by an axial symmetry, but the differentiation of its first woody bundles is centrifugal; leaves are characterized by a bilateral symmetry. He also showed that each organ of a plant includes three regions — an external envelope, a cortical or median region, and a central region. After having delimited the diverse zones in organs, VAN TIEGHEM described their characteristics and made a comparative study of them in the three members of the plant.

SACHS believed that the parts of plants may be referred to a few original "members" if due regard is paid to their development, their mutual positions, the relative order of their formation, and their earliest stages. The plasticity of the members of a plant, said he, is shown by the fact that leaves may perform, not one but many functions. A particular leaf may however perform a particular function, the nature of which is a problem for physiologists to investigate. As the process of organogeny proceeds, the morphological character of a given plant "member" is often lost, hence it is necessary to retrace the series of changes from the original form, a state in which the several members are extremely similar to one another. SACHS considered that this was a scientific concept of metamorphosis. "Metamorphosis is the varied development of members of the same morphological value resulting from their adaptation to definite functions".

Noting that the different members of a plant arise from one another by branching or by budding, SACHS conceived the idea of homogenous or heterogenous members. A root, for instance, branches in the production of new roots. A stem, however, may produce not only new stems, but leaves, roots, and hairs. But since members which are morphologically dissimilar differ from each other more in degree than in kind, the difference between branching and the production of new members must be regarded, not as an opposition, but only as a gradually increasing differentiation of the members which arise from each other.

This concept of metamorphosis is obviously based on sound scientific foundations and contrasts very sharply with that formulated by GOETHE. SACHS did agree with some of the ideas of the Nature-Philosophers in his concept of unity in diversity. A member of the plant organization is not a thing apart, something preformed and destined from the egg to be what it is and nothing else. It is something plastic, capable of growth in different ways. His ideas on the histological application of this subject will be presented in a subsequent paragraph in which meristems will be discussed.

KARL GOEBEL (1855-1932) broadened the field of organography and clarified its principles. His science of organography was based on the concept that the forms of plant members are determined by causes which may be defined by objective investigation. Morphology should no longer be kept separate from physiology. His "Organographie der Pflanzen" contains an extremely comprehensive exposition of the subject, and has been of great service in the subsequent study of morphology, because of its emphasis on the relations between organic form and function. He was from the beginning an ardent admirer of the English philosopher, HER-

BERT SPENCER. He was at one time an assistant to SACHS in harmony with whom he always maintained the dependence of form upon function.

GOEBEL considered that the fundamental problem was not phylogenetic development, but development in general. The study of ontogenetic development is more important, said he, because it permits of experimental study, and conclusions can only be accepted when they rest upon experimental proof. Since form and function are always co-determinate, a change in one leads to a change in the other. His doctrine of morphology has been fundamental to modern research in this field, especially his ontogenetic and experimental studies. He based his ideas of morphology upon the concept that the plant is a living body whose functions are intimately related to the outside world, and that all morphological characters are, or have been, adaptive.

GOEBEL employed the word "metamorphosis" to denote organic development, but not in the old idealistic sense. By it he would express the idea that a change in function produces a change in form. According to him, no "indifferent rudiment" exists, for every rudiment has its peculiar qualities, which determine its development. Leaf metamorphosis, he said, is primarily an ontogenetic process in which the path of development of originally identical primordia, *i.e.*, foliage leaf primordia, is diverted into other channels as a result of internal and external changes. The phenomenon of metamorphosis is always related to a change in function and is not limited merely to the transformation of organ primordia. Cataphylls and other diverse types of foliar structures he assumed originated from foliage leaf primordia. For this concept so fundamental to research in morphology we shall ever be indebted to GOEBEL. His healthy skepticism of the assumptions freely made about homologies and phylogenetic interpretations has kept open the paths of objective research. He used the word metamorphosis to denote organic development, not, however, in the sense of the school of GOETHE in which one specialized organ changed into another, but rather to express the idea that a change in function produces a change in form.

The concept of the meristem is so important in organography that a short discussion of some important studies will be included at this place.

NÄGELI (1817-1891), who coined the word, defined meristem as a group of cells capable of division. In this sense it is more descriptive than the "Punctum Vegetationis" of WOLFF. Morphologists soon came to a realization that here was a veritable Pandora's box out of which came the diverse elements of the plant body. NÄGELI showed (1858) that the sequence of cell divisions have great importance in determining the form of the plant member. Cell divisions are sometimes very regular and easily followed but this is not a general rule. Having been greatly impressed by the sequence of cell divisions in the apical cell of thallophytes, NÄGELI assumed that the heart of the meristem of all plants was an apical cell (Scheitelzell) and maintained that there was no funda-

mental difference in the mode of origin of apical tissues in vascular cryptogams and phanerogams. HOFMEISTER supported NÄGELI's idea, although he admitted that there would be some difficulty in proving the assumption. Subsequent work on the growing points of gymnosperms and angiosperms failed, however, to show a real apical cell.

SCHWENDENER announced that the single, three-sided apical call is the exception and not the rule in the shoot apex of gymnosperms, and suggested that the apex is frequently crowned with four equivalent juxtaposed initials.

A great impetus to the study of meristems was given by HANSTEIN when he formulated a histogenetic theory of the shoot apex. He designated (1868) the cell layers of the stem apex of angiosperms as dermatogen, periblem, and plerome and considered that they give rise to epidermis, cortex, and stele respectively. HANSTEIN's theory was a great vivifying influence on the study of morphology, bringing into the field the importance of developmental studies, a technique later emphasized strongly by GOEBEL. Furthermore it was a release from the formalism of the doctrine of a single, immortal, apical cell which had to be found even though it did not exist. HANSTEIN reported that even in the embryo of phanerogams there was no evidence of an apical cell, but on the contrary, there was at an early stage a clear differentiation into an outer layer and an inner core of tissue. His viewpoint was obviously ontogenetic, in contrast to NÄGELI's which was phylogenetic. HANSTEIN's doctrine taught that each of the layers in the shoot apex of angiosperms arose from a definite initial or group of initial cells. In other words, that a differentiation already existed in the youngest stages of the shoot apex.

It is not surprising that this histogen theory of the shoot apex of phanerogams should elicit pungent denials on the part of the men who formulated the doctrine of a single apical cell. NÄGELI was especially outspoken in his opposition to the histogen theory.

SACHS accepted the histogen theory but conceived that the differentiation rested on a physiological basis. He postulated three systems of tissues — epidermal, fascicular, and fundamental, the latter lying between the first two.

SACHS also adopted NÄGELI's classification of tissues as meristems and permanent tissue, emphasizing, however, that it does not wholly depend upon the age of the cells. He distinguished two classes of growing points — one with an apical cell (usually the cryptogams) and the other without an apical cell (as in phanerogams) but was not inclined to attach undue importance to the differences, adding,

> "But whenever a differentiation of tissues of this kind occurs in a plant, it only takes place progressively; originally the whole mass of the growing portion of the plant (stem, leaf, or root) consists of a uniform tissue out of which, by diverse development of its layers, these tissue-systems have their origin. This tissue of the youngest parts of plants which is not yet differentiated may be termed Primary Tissue, or since its cells are always capable of division, Primary Meristem".

The HANSTEIN concept of the shoot apex prevailed for some time although the validity of the histogenic layers could not be established in all plants. KOCH proposed a new classification in

1891 according to which there were only two embryonic zones, *viz.*, an outer mantle of cells containing dense cytoplasm, and an inner core of cells containing vacuolated cytoplasm which absorbed dyes with less avidity than those of the outer mantle. The inner core of cells produced only the pith, while the outer mantle produced epidermis, cortex, procambial tissue, and leaves. He concluded that the meristematic tissue of the apex grows as a whole and that HANSTEIN's histogenic layers have no real existence.

Since 1924 the histogen theory has been generally replaced by the Tunica-Corpus theory of SCHMIDT. This appears to be the most satisfactory concept of the shoot apex of angiosperms yet formulated. According to its author, the "tunica" consists of the outer meristematic layer or layers of cells, and the "corpus" is the central meristematic aggregation of cells in which divisions occur in many planes. The theory of shoot apex organization is not formalized, on the contrary, it is non-committal concerning the future derivatives of the meristematic tissues. It emphasizes the developmental rather than the structural processes of apical growth. The "tunica" is regarded as an enveloping layer consisting of one or more layers of cells which divide generally, but not always, by anticlinal walls. The "corpus" is regarded as a growing mass of undifferentiated cells which divide in many planes, and thus contribute to the mass of the stem. The investigations of FOSTER have shown that the shoot apices of border-line plants like gingko and cycas have a unique type of apical structure. The "central mother cells" of the apex resemble to a great extent the cells at the summit of the apex of certain vascular cryptogams. Obviously no rigid morphological concepts will apply to all groups of plants.

Physiological anatomy:- The work of VÖCHTING (1847-1917) which appeared in 1878 was an organographic rather than an anatomical approach to the problem of morphogenesis, although some attention was necessarily paid to the cell theory. In so far as possible VÖCHTING undertook to investigate the effects of internal and external factors on the formation of organs on isolated parts of plants. He brought a fresh, new method of attack to the problem of morphogenesis, in contrast to much of the contemporaneous work which hung on the idealistic pegs of classical morphology. His work on organ-formation led to the idea of a definite orientation of factors in the plant which presided over the processes of bud development, of root formation, and of complex interrelations between parts.

It is gratifying to see how VÖCHTING surpassed the achievement of so keen-eyed a man as HOFMEISTER who had published his work "Allgemeine Morphologie der Gewächse" 10 years earlier. HOFMEISTER had been able to formulate such concepts as "shoots of varying dignity", "extension of the embryonal elements in the growing point", "adventitious shoots", "spatial relationships of lateral shoots", etc. but out of it came no such comprehensive view of the problem of morphogenesis as VÖCHTING gave. By oft-repeated experiments he clearly established the existence of specific growth responses in the morphologically apical and basal regions of stems, roots, leaves, and fruits. He interpreted these to mean that there was a definite "polarity" in the plant, meaning that

there was an undetermined factor which regulated the growth of axial organs somewhat as the forces in a bar of metal determine its magnetic properties. He showed that each isolated piece of shoot is the bearer of a force which endeavors to form shoots at the tip, and roots at the base. The magnitude and nature of this force naturally varies according to the age and the structure of the shoot. He concluded his physiological-morphological work with a chapter on the physiological individuality of the organism which emphasized the organogenetic problems of plant growth. Admitting that the cause of growth is unknown, he emphasized that inherent forces in the organism operate to produce an orderly distribution of matter in space and time.

The study of physiological anatomy of plants which began about 1870 emphasized another phase of morphology and anatomy. To a certain extent the study of any problem in anatomy involves physiology and the concept of physiological anatomy is somewhat hard to define.

SCHWENDENER (1829-1919) opened the way for the study of physiological anatomy by the publication in 1874 of his theory of the mechanical principle in the structure of monocotyledons. Although it is not a profound discussion of stem structure it appears to have motivated others who went further into the causal relations between stem structure and physiological functions. SCHWENDENER dwelt at length upon the similarities between the structure of stems and of beams, girders, etc. referring the arrangement of the woody tissues to the conditions imposed by the environment.

SACHS' (1832-1897) pertinent discussions on the role of tissue tensions in growth emphasized the importance of turgor in promoting and directing the growth of organs and commented upon the relation of turgidity to organ structure. Thus the ideas of SCHWENDENER were extended. SACHS referred the formation of annual rings in the wood of trees to the retarding effect of external pressure on the cells. He reported that the pressure in the spring was less than in the fall, thereby permitting the formation of wood cells with larger lumina in the spring. He also discussed the influence of light and gravitation in determining the growth of plants, resulting in the familiar shapes of symmetry and dorsiventrality. External conditions may also influence growth indirectly by affecting the formation and transport of necessary materials. SACHS recognized that there are contrasting internal conditions which are inherent in the organization of the plant and which are generally termed hereditary. He envisioned the reality of the internal factors governing specific and determinate organization but was naturally unable to determine their nature.

The name of HABERLANDT (*b.* 1854) will be at once associated with the development of physiological plant anatomy. The first edition of HABERLANDT'S "Physiologische Pflanzenanatomie" appeared in 1884, the sixth in 1924. He gave a refreshing exposition of the anatomy of plants in relation to physiological functions without, however, entering the physiological field as SACHS had done. He named twelve anatomico-physiological systems (meristematic, tegumentary, mechanical, etc.) without attempting to demarcate their ontogenetic or phylogenetic relations. The storage systems might be in one case stems, in another, bulbs, in another tubers. His analysis of relations between structure and

environment has proved useful in physiological ecology in relation to the adaptations observed in various habitats. HABERLANDT's classification of the elements of the conducting systems is in contrast to that formulated by morphologists, and has not been generally adopted. He recognized three: (1) the leptome, consisting of protein conducting elements (sieve tubes, and companion cells, and possibly cambiform cells); (2) the hadrome, consisting of water conducting vessels and tracheids; (3) the mestome, or conducting bundle, consisting of the leptome and hadrome. In most cases each vascular bundle is enclosed within a bundle sheath composed of parenchymatous cells which he regarded as conducting parenchyma. Without introducing any essentially new material, HABERLANDT gave a rational discussion of the "Ventilating System" of the plant, in which he emphasized the importance of open channels for the gaseous interchanges with the surrounding air. It will be recalled that MALPIGHI had been greatly concerned with this problem.

A philosophical discussion of the problem of size and form in plants by BOWER brought together (1930) in a comprehensive way the morphological and physiological relations of the evolving plant kingdom. In place of the earlier didactic discussions of the size-form relations of plants, BOWER wrote of the plasticity of form and structure in relation to size, showing how the phylogeny of the plant as well as the physiological processes have operated to produce what we now have in the plant kingdom. He believed that form in relation to size is due only partially to the conditions during individual development. Nevertheless, throughout the evolution of any given race, susceptibility to the conditions of the environment has existed and will have had cumulative effect in producing the results now manifest. The obvious trend towards larger plant bodies in the process of evolution naturally imposed severe conditions on the development of the absorbing, ventilating, and photo-synthesizing systems. BOWER advanced the idea that changes in contour, either of internal or external surfaces, are proportional to the area exposed. He emphasized that it was the success of the higher land plants in adapting their structure to their size - factor requirements which made possible their continued growth. Phylogenetically they started with a simple organization and developed an apparatus which allowed them to carry out the functions of a small, simply organized plant. Consequently the three morphological factors which have greatly contributed to the success of massive plants are continued embryogeny, internal ventilation, and cambial activity. BOWER placed the origin of the first factor early in phylogenetic history, the origins of the other two came later. The last two are important because they provide an automatically increasing surface of exposure both of the tracheal elements to living cells, and of internal cells to the atmosphere. Meanwhile the endodermis was obliterated by the consequences of secondary growth in many plants. These relatively few types of changes made possible the continuance of the necessary physiological processes, thus allowing increases in size of the spermatophytes until the limit of mechanical resistance was reached.

BOWER's synthesis of the elements of the physiological and morphological relations of the plant and his adherence to known factors make his discussion an important contribution.

Morphology of the flower:- The tantalizing complexities and almost bewildering variations in structure of the angiosperm flower have been assiduously studied, but morphologists still differ in their interpretations of its structure. It would seem that TENNYSON's soliloquy on the mystery of the "Flower in the crannied wall" is as much of a problem as ever.

The problem was first attacked by the idealists and later by the mechanists, each of whom conceived of the flower in his own way, often to the exclusion of all other ways. GOETHE seems to have considered the flower as a unit structure, a modified vegetative shoot, in which each part of the flower corresponded to foliar appendages of the shoot. The floral organ had thus arisen by a metamorphosis of the vegetative shoot and its organs. GOETHE's "foliar theory" of the nature of the flower formulated on the basis of resemblances is held today by some, but sharply challenged by other morphologists. The organographic approach which appears to have been inherited from GOETHE's ideas of archetypes and metamorphosis was to him the logical approach.

Inspired by the doctrine of organic evolution, EICHLER (1839-1887) investigated the floral anatomy of each natural order and of each of its subdivisions and published them under the title "Blüthendiagramme" (1875-8). His extensive descriptions of the types of flowers were eagerly read by some, but ignored by others. EICHLER's elaborate system of diagrams of floral architecture was based mainly upon the resemblances of structure found in families and genera. In his "Blüthendiagramme" he unmistakably based interpretations on evolutionary concepts. From it no important conclusions were obtained which answered the question "What is a flower?"

The earlier view of floral morphology was gradually modified, chiefly due to the influence of GOEBEL, to regard the flower as a shoot bearing sporophylls. GOEBEL showed that sporangia are sometimes produced on normal green leaves of *Botrychium* (accompanied by a reduction in the size of the leaf) and concluded that sporophylls are metamorphosed foliage leaves. Furthermore, the discovery of the significance of alternation of generations brought a realization that stamens and carpels, since they are concerned in spore production, are not truly sexual organs. BOWER modified the theory of floral metamorphosis in a different way. Having studied the sporebearing members of the pteridophytes, he formulated a concept of the origin of flowers from a sporangial or strobiloid form, in which the formation and distribution of sporangia were the important considerations. According to BOWER sporophylls antedate foliage leaves in such a strobiloid form. If there has been a process of metamorphosis it has resulted in the sterilization of the outer sporophylls, by which the organs of the perianth were produced. BOWER's theory of segregation has proven to be of great value in clarifying this situation. BOWER concluded that the whole shoot of relatively primitive vascular plants was nonspecialized, serving both vegetative and propagative functions. In the course of evolution one part of the shoot became exclusively vegetative, while another produced sporangia. There has been, therefore, a process of segregation between vegetative and reproductive functions rather than metamorphosis of relatively unspecialized rudiments.

The "foliar theory" has been elaborated in one form or another. AGNES ARBER (*b.* 1879) has interpreted (1937) the flower in a holistic sense, suggesting that it is comparable to a vegetative shoot in a condition of permanent infantilism. She thus summarized her views:

> "Morphology may be considered as the study of the plant as a whole under the aspect of form . . . the word form being used not only in its more obvious meaning, but also to include the entire organization, external and internal, from the beginning to the end of the life history".

She did not believe that phylogeny is capable of solving the fundamental problems of floral morphology.

Another group of morphologists, of whom EAMES (*b.* 1881) is representative, has investigated the anatomical structure of the flower and of its organs, finding therein support for the foliar theory. EAMES defined (1925) a flower as "A typical stem with appendages; in no fundamental way does it depart structurally from the normal stem with leaves". He found that the number of vascular traces diverging from the axis to the floral parts of angiosperms is normally constant, that is, there is usually one trace to the stamen, one to the petal, three to the carpel, and the same number to the sepal as to the leaf. The single traces seem to represent the remains of fusions of the vascular strands. These fusions have often occurred between floral parts and their vascular strands.

Miss SAUNDERS (*b.* 1865), investigating the homologies in the anatomy of the flower, found that the floral traces are arranged in spirals and whorls. The transition from spiral to whorl is accomplished by a breaking and flattening of the spiral. Each type of floral structure is said to have a midrib which comes off the stele in whorls and spirals corresponding to those of the floral parts. Some variations occur, as in cases where the vascular strands come off the stele inwardly, breaking the pattern or, rather, making it less marked.

The greatest difference of interpretation between SAUNDERS and EAMES is in the interpretation of the carpel. Based upon a study of stocks and other plants, where the number of valve carpels is reduced, polymorphism (a consolidation of the valve carpels) has occurred. Based upon a study of stocks and other *Cruciferae*, SAUNDERS formulated the idea of carpel polymorphism in which there are two types: valve and consolidated. In the *Cruciferae* and other plants, where the number of valve carpels is reduced, polymorphism (a consolidation of the valve carpels) has occurred.

GRÉGOIRE (1870-1938) concluded that flower and vegetative shoots belong to fundamentally different categories and that the former was not derived from the latter. The center of growth in the vegetative apex is in a group of cells inside the parenchymatous corpus, a short distance below the surface. Growth of the floral apex, according to GRÉGOIRE, is due to the multiplication of embryonic cells in the superficial "manchon méristématique", or embryonic muff, which has no definable group of meristematic initial cells. In the shoot apex vascular strands differentiate at the base of the leaf initial both toward the meristem ring and toward the tip of the leaf initial, *i.e.* basipetally and acropetally. In the floral apex, vascular strands come off the stele without reference

to the initial floral parts and vasculation proceeds acropetally. GRÉGOIRE concluded that in the flower the tip of the axis is always entirely used up to form carpels, no residual apex being found and that the contrast is seen in the vegetative shoot where the apex extends beyond the bases of the leaf initials.

The histogenetic approach has also been utilized (1928) by TROLL who maintained that GOETHE was essentially correct in stating that morphology is comparative morphology. The "Gestalttypus" according to TROLL is exemplified by four types: (a) part of a single flower, (b) a single flower, (c) an inflorescence, (d) or an inflorescence of inflorescences. TROLL regarded floral organs as essentially foliar. The carpel is formed from peltate leaves by an infolding of the margins. He elaborated the idea and showed how the folding of the carpels may account for the various types of gynoecia. TROLL's doctrine is the more remarkable when it is remembered that he supported it by his histogenetic studies.

The morphology of the flower has also been studied (1933) from the palaeontological approach by HAMSHAW THOMAS who considered that the foliar theory proved unsatisfactory. He believed that the *Caytoniales,* which have pinnate megaspore-containing branches, are similar to the ancestor of modern angiosperms. The megasporangium, or seed, was at first single and partly covered with a cupule; as development proceeded the seeds became more numerous and better covered by the cupule until it entirely enclosed them. Then two branches and their cupules fused to form a carpel, the carpel wall consisting of fused cupules and the placentae of fused cupules and the tips of branches, the branch tips forming the stigmatic surfaces. These conclusions are clearly at variance with GOETHE's theory.

Another concept (1936) which is in direct antithesis to the original idea of GOETHE and the resulting school of thought has been propounded by JOHN MCLEAN THOMPSON, who emphasized the point that progress in floral morphology has been impeded by the arbitrary assignment of floral organs to foliar categories. Using GRÉGOIRE's "manchon méristématique" he suggested that perhaps in the future this "muff" will be looked upon as having fundamentally a sporogenous function — spore production. Progressive sterilization has produced the sterile portions of the androecium and gynoecium; the perianth representing complete sterilization.

Again, he summarized (1937) thus:

> "We are left with what appears to be as near an approach to an essential conception as our knowledge of heterosporous land plants has yet offered, namely that of a heterosporous axis with microsporangia and megasporangia in ascending succession".

According to THOMPSON such a conclusion is based upon the complete ontogeny of the flower — from inception to senescence. He considers any study of ancestral types as a means of interpreting angiospermy, as known in Angiosperms, to be beside the point until the so-called "state of angiospermy" is clearly perceived.

Recapitulation:- The progress of plant morphology since the ground-breaking work of CASPAR FRIEDERICH WOLFF has been slow in spite of the assiduous work of many investigators. At times

its progress has been seriously hampered by the intrusion of speculation which stifled instead of vivifying investigation. Recoiling from the doctrines of idealistic morphology investigators have, nevertheless, repeatedly launched new attempts to determine objectively the actual nature of the plant and its parts. Students of thallophytes and bryophytes perhaps had the easiest task because they could study the whole life cycle of these relatively simply organized plants, but students of the archegoniates and higher plants, from the beginning found their work beset with difficulties. The chaos of ideas was somewhat clarified by the discovery that the alternation of gametophytic and sporophytic generations is such a general character in the plant kingdom, but there are still many unanswered problems.

Morphology involuntarily acquired many of the problems which baffled taxonomists and later was loaded with problems for which evolutionists demanded answers. Once the door had been opened no one was found who could shut it. If it be assumed that plants of the modern world have descended from common ancestral forms, can it be assumed that they possess homologous organs, or will it be found that they have undergone such transformations that homologies can be found only in closely related groups? Many morphologists are still skeptical about the results of phylogenetical theories on account of the serious gaps in the line of descent. The general comment on such work is "Interesting, if true".

Anatomical researches have tended to unify the various concepts of plant organization and structure, on the contrary, physiological and organographical researches have tended to dispell the ideas of phylogenetic homologies by their insistence upon the relation between form and function. The formulation of the concepts of plasticity and response in plant development was a vivifying influence in the study of morphology.

The student who surveys the history of plant morphology must be impressed by its gradual emancipation from teleology as the science has developed. That life forms have evolved under the changing conditions on the earth cannot be gainsaid, nor can one contradict the evidence that new form relations have had survival values. But, as GOEBEL said, the complexity of forms is greater than that of the environment, and he was accordingly skeptical about the formation of organs in response to a need for them. The substantial progress in morphology has come from studies on the developmental phenomena and this applies particularly to ontogenetic development.

Floral morphology appears to be the *bête noir* of morphological botany to judge from the divergence of interpretations in the literature on the subject. GOEBEL's doctrine that the sporangia are organs *sui generis* as much as shoots, or roots is a cornerstone that is not likely soon to be displaced. To a certain extent it is supported by GRÉGOIRE's conclusions.

REFERENCES:-

BOWER, F. O. (1930): Size and form in plants. Macmillan, London.

—— —— (1939): Botany of the living plant. 3rd edition, Macmillan, London.

CAMPBELL, D. H. (1895): Structure and development of mosses and ferns. Macmillan, London and New York.

de Bary, A. (1877): Vergleichende Anatomie der Vegetationsorgane der Phanerogamen und Farne. Engelmann, Leipzig. (Comparative anatomy of the vegetative organs of the phanerogams and ferns, transl. by Bower and Scott, 1884. Clarendon Press, Oxford).

de Candolle, A. P. (1813): Théorie élémentaire de la botanique. Paris.

—— —— (1827): Organographie végétale. Baillière, Paris.

Eames, A. J. and MacDaniels, L. H. (1925): Introduction to plant anatomy. 1st edition, McGraw-Hill, New York.

Foster, A. S. (1939): Problems of structure, growth, and evolution of the shoot apex of seed plants. Bot. Rev. 5:454-470.

Goebel, K. (1882): Outlines of classification and special morphology of plants. Clarendon Press, Oxford. (Eng. transl. by Garnsey, 1887).

—— —— (1898): Organographie der Pflanzen. Fischer, Jena.

—— —— (1924): Wilhelm Hofmeister. Leipzig. (Eng. transl. by Bower, 1926. London).

Haberlandt, G. (1904): Physiologische Pflanzenanatomie. Dritte Auflage, Engelmann, Leipzig. (Transl. by Drummond, 1914. Glasgow).

Hofmeister, Wilhelm (1851): Vergleichende Untersuchungen. Leipzig.

—— —— (1868): Allgemeine Morphologie der Gewächse. Engelmann, Leipzig.

Sachs, Julius von (1874): Lehrbuch der Botanik. Engelmann, Leipzig. (Transl. by Vines, 1882. Clarendon Press, Oxford).

Thompson, John McLean (1937): On the place of Ontogeny in floral enquiry. Hartley Bot. Lab. Publ. No. 17, Liverpool University.

Chapter XI.

CYTOLOGY.

Botany had a great development in the 17th and 18th centuries and the ripened fruits of that era were the precursors of a 19th century of progress in the study of the inner characters of plants. The cellular structure of wood and cork had been discovered by microscopists in the 17th century, and the name "cell" had been applied by HOOKE. The anatomists MALPIGHI and GREW also saw cells and recognized them as units of tissues, but saw little that was within the rigid walls. More than a century passed before gifted men turned their attention to these little units of the organism.

MIRBEL and LAMARCK had recognized the importance of cellular organization in the structure and development of organisms, but DUTROCHET first emphasized the individuality of the cell. In 1824 he wrote "This astounding organ is truly the fundamental element of organization; indeed, everything in the organic tissues of plants is evidently derived from the cell, and observation has proven that it is the same with animals".

The science of cytology was born in the fourth decade of the 19th century when a group of extraordinarily brilliant men, skillful in the use of the microscope, and logical in their approach, began new studies in the anatomy and physiology of plants. The formulation of the concept of the cell as the unit of organic life was one of the great biological triumphs of the 19th century. Once the technique of cytology had been discovered, science fairly leaped forward into myriads of new paths.

The Cell Theory:- The inception of the new period was the discovery of the cell nucleus by ROBERT BROWN, who has already been mentioned as an explorer of the Australian flora. In 1831 he announced in a paper contributed to the Linnean Society of London that he had seen a single circular areola in cells of the epidermis and parenchyma of certain orchids, as well as in the cells of other plants which were relatively free from granular matter. BROWN's concise description is so exact that there has never been the slightest doubt about the identity of the cell structure which he saw.

The matter might have rested there for a long time had it not been taken up by M. J. SCHLEIDEN (1804-1881), professor at Jena, whose treatise "Beiträge zur Phytogenesis" was published in 1838 and is regarded as the foundation of the cell theory. Although he was wrong in some fundamentally important matters, his concept of the prime importance of the nucleus in the propagation of cells was correct up to a certain point, and this brief publication has exerted a tremendous subsequent influence on plant and animal biology. SCHLEIDEN fastened on the cell theory the false idea that new cells were derived by budding from the nucleus, which

he therefore called the cytoblast; *i.e.*, cell-bud. He believed that the nucleus rose from the mucilaginous substance of the cell and that it might later be absorbed into the common mass of the sap.

THEODOR SCHWANN (1810-1882), professor in the university of Louvain and later at Liège, was impressed with SCHLEIDEN's theory of cell formation and set himself to the study of the animal tissues. SCHWANN and SCHLEIDEN worked sympathetically on the important problems and are to be regarded as co-founders of the cell theory. SCHWANN said:

> "The cell nucleus is usually dark, granulous; often somewhat yellowish; but some occur which are quite pellucid and smooth. It is either solid, and composed of a more or less minutely granulated mass, or hollow".

VON MOHL (1805-1872) made far more exact and painstaking studies on the cell than any of his predecessors, yet, even he, was not too definite about the multiplication of nuclei. He thought that the process of free cell formation was more prevalent than it really is, and was uncertain whether the process of nuclear division can be repeated indefinitely. He wrote (1851):

> "The second mode of origin of a nucleus, by division of a nucleus already existing in the parent-cell, seems to be much rarer than the new production of them, for as yet it has been observed only in a few cases . . . NÄGELI thinks that the process is similar to that in cell division, the membrane of the nucleus forming a partition, and the two portions separating in the form of two distinct cells. I was quite unable to see such a membranous septum and a membrane on nuclei generally. The division appeared to me to take place by gradual constriction. HOFMEISTER thinks that the membrane of the nucleus dissolves, but its substance remains in the midst of the cell; a mass of granular substance accumulates around it which separates, without being invested by a membrane, into two masses, and these afterwards become clothed with membranes and appear as two daughter-nuclei."

We surmise that these cytologists had difficulties in distinguishing the contents of cells when we note that VON MOHL stated that the number of nuclei that are formed in a cell varies from two to six or more.

W. HOFMEISTER (1824-1877) refuted SCHLEIDEN's theory of cell formation as buds from the nucleus and proceeded in 1849 to describe the behavior of the nucleus in cell formation and the production of new walls. He announced definitely that the nucleus of the mother cell divided into two, and that half the contents of the cell collected around each of the daughter nuclei. He demonstrated the nuclear membrane and found that before the dissolution of the nucleus (as then assumed) this membrane and the nucleoli vanish. He mentioned the "granular plate" between the two daughter nuclei and evidently saw chromosomes. Be it remembered that he saw and studied all these structures without fixing and staining the materials.

For some time the nucleus was thought to be a vesicle containing fluids of unknown composition. Eventually it was discovered that its form and size are of less importance than certain substances which it contains. Even the arrangement of these substances is intimately related to the activity of the nucleus.

About 1844 NÄGELI and VON MOHL simultaneously began to publish papers which dispelled many of the misty ideas about cells. Independently they distinguished the cell wall from the cell contents. They recognized the "primordial utricle" (cytoplasm), for

which VON MOHL, as early as 1846, had used the term protoplasm which had been coined by the Bohemian naturalist, JOHANNES EVANGELISTA PURKINJE (1787-1869). VON MOHL wrote "This fluid is colored yellow by iodine, coagulated by alcohol and acids, and contains albumen in abundance, whence young organs are always rich in nitrogen". He perceived that protoplasm was a peculiar substance distinct from the other contents of the cell and explained the part it plays in cell division. We owe the concept that protoplasm is the physical basis of life to MAX SCHULTZE (1825-1874) and that it is essentially similar in all living organisms. It then became evident that the rigid wall which had been studied by HOOKE and others was not the vitally important part of the cell. Nevertheless the term cell has been retained, HERTWIG says, "partly as a symbol of loyalty to those vigorous combatants, who, as BRÜCKE expresses it, conquered the whole field of histology under the banner of the cell theory". SCHULTZE defined a cell as "A small mass of protoplasm endowed with the attributes of life". It is perfectly clear that neither he nor any other investigator implied that the cell is a simple matter. The physiologist BRÜCKE concluded that protoplasm must possess an exceedingly intricate structure which baffled the available means of observation. He very pertinently designated the "ultimate particle" of animals and plants, that is to say the cell, as the elementary organism.

SCHLEIDEN's comprehensive book "Grundzüge der wissenschaftlichen Botanik" (1849) summarized his views on the nature of the cell and gave his readers a new statement of the cell theory. He criticised harshly many of his predecessors, but at any rate he cleared the air of many misconceptions. He showed the tremendous importance of this doctrine for understanding the salient aspects of living things and how completely the organism is dependent upon the varied activities of these living units. The validity of the cell doctrine is evident from the way in which it unlocked many closed doors. Of great importance also was VON MOHL's "Die vegetabilische Zelle" (1851). Further researches were needed to elucidate the role of cells in connection with development and inheritance and the end has not been reached even after a century of intensive study, but the formative period was between 1831 and 1851.

Motility of cell contents had been known since its discovery by CORTI (1774) and its rediscovery by TREVIRANUS (1807) in *Chara*. VON MOHL described not only the streaming movements, but the radial arrangement around attraction centers, the movements of cilia and flagella, and muscular contraction, but without assigning any cause of the motion. QUINCKE and BÜTSCHLI and others investigated the movements in emulsions of oils, obtaining results of great scientific interest, DARWIN clearly described (1875) the mutability of cell contents in *Drosera* leaf tentacles and commented on the rapidity of the changes in what he called "Aggregation of the protoplasm" (see quotation on a subsequent page). These "masses" of protoplasm were shown by DE VRIES to be drops of vacuolar solution surrounded by protoplasm.

Plasmodesmata, or threads of protoplasm which connect neighboring protoplasts, were discovered by TANGL in 1879, and subsequently carefully investigated (1901) by STRASBURGER and others. PFEFFER (1896) believed that these threads facilitate the trans-

mission of stimuli from cell to cell. SHARP (1926) suggested that they are in part responsible for the readiness with which nutritive materials are translocated in storage tissues.

The structure of protoplasm:- Cytologists attempted to obtain a concept of the physical structure of protoplasm. The early work was done principally with animal cells.

The fibrillar theory which held that fibers arise from the nucleus and radiate through the cell was advanced by the researches of FROMMANN (1867), PFLÜGER (1869 and 1871) and HEIDENHAIN (1868), and later was developed by FLEMMING (1882).

The granular theory maintained that granules are the essential constituents of protoplasm. They were designated "microsomes" by HANSTEIN. ALTMANN (1886) who supported the theory believed that the granules were really living entities, homologous with bacteria. Although fallacious, this homology opened the way for a differentiation between the cytoplasm and its inclusions.

The alveolar theory was formulated in 1878 by BÜTSCHLI who expressed the opinion that the reticular structures might be alveolar, or foam-like. Later he amplified the theory with which his name has long been associated. STRASBURGER seemed to agree that the structure of protoplasm was reticular, but if one examines the figures in his published work it will appear that he represented protoplasm as a tangle of short twisted fibers, after the manner of FLEMMING.

NÄGELI's theory of the idioplasm has now mainly an historical interest because of his attempt to relate the structure of protoplasm to phylogeny. The theory had the virtue of being indefinite enough to make opposition difficult, while at the same time it was definite enough to be related to things which one could see in the cell. NÄGELI believed that each body of idioplasm consists originally of only one group of micellae; as it grows in size it breaks up into several groups. As growth proceeds, the process is repeated, giving rise to new configurations in which there are new combinations of forces, and the body of idioplasm becomes chemically and morphologically more complex. This constituted what NÄGELI called "the automatic perfecting process", or progression of the idioplasm, and entrophy of organic matter.

NÄGELI thus formulated clearly the idea that there are different kinds of protoplasm, and that one of them (the "idioplasm") is primarily responsible for hereditary characters. His other idea that the determinants may be composed of relatively simple units combined in various ways anticipated some of the commonly accepted theories of the next century concerning the vectors of hereditary factors.

The response of the living protoplast to various factors was observed by the first cytologists who worked so extensively on living cells. HOFMEISTER described (1867) the effects of injurious chemicals on the motility and distribution of protoplasm within the cell, KÜHNE demonstrated (1864) the change from delicate strands to globular aggregations when cells of the stamen hairs of *Tradescantia* were stimulated by the passage of an electric current. PRIESTLEY concluded (1930) that protoplasm has a seasonal change in its aggregation condition, whereby the winter gel of the cambial protoplasm changes into a sol in the spring.

DUFRÉNOY has shown (1935) that invasion of parasitic fungi, virus diseases, toxic salts, mechanical injuries, and unfavorable temperatures, generally produce phenomena similar to those which DARWIN had described as "aggregation". DUFRÉNOY emphasized the importance of factors which tend to conserve a certain architecture in the labile cell constituents, especially as they affect the interfaces between cytoplasm and vacuole or between cytoplasm and mitochondria.

The cell wall:- The early cytologists were justly perplexed by the extraordinary diversity of form and substance of the cell wall. Most botanists writing prior to 1840 were silent on the subject of the growth of the cell wall. PAYEN (1844) determined that the membrane of all young cells consists of cellulose in a comparatively pure state. In his opinion, the membranes of older cells are combined more or less with other organic or inorganic compounds, through the presence of which the physical and chemical properties of the cell membranes undergo alterations. SCHLEIDEN in his "Grundzüge" devoted about 50 pages to discussing the form and size of the individual cell and concluded that the wall is formed in some way by the activity of the contiguous cytoplasm. Aside from his statement that the wall in its original form is cellulose, he had little to say about composition. Iodine and sulphuric acid were the reagents in common use, and most of the investigators then walked by faith and saw but little. The character of fungus-cellulose was demonstrated by DE BARY (1884) and VAN WISSELINGH (1898) showed that it consisted largely of chitin.

NÄGELI described what he regarded as a second type of wall formation, based on a study of pollen mother cell development. His were the first conscious attempts to refer growth to molecular processes and his conclusions retain great theoretical importance, although based largely on the erroneous assumption that the growth of starch grains takes place by intussusception. NÄGELI's theory of growth by intussusception was eventually challenged by STRASBURGER who advanced evidence that cell walls grow by apposition and therefore have a laminated structure. Ultimately STRASBURGER adopted a theory which involved the presence of protoplasm in the wall through which new materials could be introduced, but not in the precise way that NÄGELI had described. TUPPER-CAREY and PRIESTLEY (1923) and DAUPHINÉ (1934) concluded that the existence of protoplasm in the cell wall is highly probable. VON MOHL (1851) held the theory that secondary cell walls had a fibrous structure, "Since their molecules are connected more firmly in the direction of a spiral than in any other direction". In recent years VON MOHL's theory has received remarkable confirmation from the results of X-ray studies on cell walls. SPONSLER, SPONSLER and DORE, and MEYER and MARK, in a series of papers published since 1924, have shown that the cellulose wall of fibers consists of glucose residues linked together in long chains which extend lengthwise of the fiber, parallel and uniformly spaced. The chains may possibly have a length equivalent to 500 to 1000 glucose units.

SPONSLER's observations (1931) on the wall of the alga *Valonia* justify the conception that the wall is composed of very thin, microscopic lamellae, probably some of them just below visibility. The lamellae extend tangentially around the wall, forming concentric layers. The distance to which they extend tangentially was not determined, but may be part way or completely around the cell. In each lamella the glucose residues are arranged to form the cellulose lattice. SPONSLER and DORE concluded that new glucose residues are added to the inner face of the cell wall where it is in contact with cytoplasm, hence growth of the cell wall is by apposition.

BAILEY concluded (1939) that cell walls have a visibly laminated structure in which cellulose is present as discreet but coalescing fibrils varying in size and porosity according to environmental conditions during formation. Lignin and other cell wall constituents penetrate the pores of the cellulose matrix and form independent matrices of their own.

While cytologists were observing the finer structure of cell walls, the chemist EDMOND FRÉMY (1814-1894), made an important contribution to the knowledge of their chemistry. He demonstrated (1840) that the hardness of unripe fruits is due to the presence in cell walls of a substance designated pectose. He reported that he had proof, at that early date, that pectose is a substance distinctly different from the pectin obtained from it by acid hydrolysis, and that it is not an insoluble calcium salt of pectin.

Modern chemists have classified pectic substances as:— (1) protopectin, formerly called pectose, is the insoluble form which occurs in unripe fruits and in other parts of plants; (2) pectin is a term used to designate the soluble pectic substances which occur naturally in juice of ripe fruits, or are obtained artificially by the action of mild hydrolytic agents upon protopectin; (3) pectic acid occurs naturally in overripe fruits and vegetables and may also be obtained by subjecting pectin to hydrolysis. Chemists believe that the chief constituent of pectin is a chain-membered polysaccharide consisting of partially esterified units of galacturonic acid.

By means of chemicals and stains MANGIN studied (1892 and 1893) the distribution of cellulose and pectosic substances in cell walls and found them to be very intimately connected. Protopectin and pectic acid were evident in walls of parenchyma, meristematic tissues, collenchyma, and bast. His work considered also the relation of protopectin to the development of wall from the cell plate. DEVAUX demonstrated (1896) that protopectin plays the role of an insoluble acid which is able to combine with kations in aqueous solution or even from salts. FARR reported (1934) the isolation of ellipsoidal particles 1.5μ in length and 1.1μ in diameter by treating cellulosic fibers with pectin solvents. These particles are composed of cellulose and are free from pectic material. The diffraction patterns given by X-ray exposure are the same as those of untreated cellulose, but with sharper lines. FARR concluded that there is no evidence for the existence of smaller micellar units, and that these particles, and not the micellae, are the actual structural units of cellulose. The validity of FARR's interpretations has been questioned by other workers who believe that the alleged

ellipsoidal particles have no existence in the plant tissue, being produced by the rather drastic treatments which were used for their isolation. Further work will doubtless clear up the difficulty in interpretation.

Advances in the knowledge of the nucleus:- The decade from 1870 to 1880 saw great advances in the knowledge of the nucleus due, in part, to the researches of SCHNEIDER, FOL, AUERBACH, BÜTSCHLI, STRASBURGER, HERTWIG, FLEMMING, VAN BENEDEN, RABL, and BOVERI. They demonstrated that as the cell is never spontaneously generated, but is produced directly by the division of another cell, so also the nucleus is never created *de novo,* but is derived from the substance of another nucleus. The problem of the nature of the nucleus was attacked simultaneously by botanists and zoologists with profit to the entire biological realm.

In view of the great importance of his work, a short biographical note must be inserted concerning EDUARD STRASBURGER (1844-1912) who was born of German parents at Warsaw and educated at Bonn and Jena. In 1869 he became professor of botany and in 1873 director of the botanical garden in Jena. He went to Bonn in 1880 as successor to HANSTEIN. In that university he created a great center for cytological research to which students went from all parts of Germany as well as from foreign countries. Frequent references to his discoveries will be made in the course of this review, showing how he broadened the investigations started by HOFMEISTER on the alternation of generations, and how he described accurately the embryo sac in gymnosperms and angiosperms, later demonstrating double fertilisation in angiosperms. STRASBURGER's "Zellbildung und Zelltheilung" published in 1875 and subsequent contributions to the subject of nuclear organization and mitosis were the road finders for all subsequent travellers in that province of cytology. His success was in part due to the perfection of the microscope and in part to methods of cytological technic. Especial attention was also directed to the problem of the achromatic thread, which forms the spindle shaped structure, and its eventual role in the formation of the cell plate. In addition to his own researches he wrote the useful "Botanisches Praktikum" which went through many editions and was translated into other languages. In coöperation with NOLL, SCHENCK, and SCHIMPER he wrote the famous "Lehrbuch der Botanik", which also went through many editions and in translations. Finally, his beautiful book of Riviera Travels rounded out his contributions to the enrichment of human thought.

FLEMMING published (1879 also 1882) a description of the process of indirect cell division with accurate figures of nuclei at various stages of division. His contributions to the technic of fixing and staining must also be mentioned. In 1880 he discovered the longitudinal splitting of the chromosomes in the dividing nucleus and in 1882 came to the conclusion that each daughter nucleus received one half of each of the chromosomes of the mother nucleus. The correctness of this conclusion was verified for plant cells by E. HEUSER, and by GUIGNARD (1883). The great import for cytology of this quantitative division of the nuclear components was promptly realized. Since the divisions are equational, each of the daughter nuclei are similar to each other and to the

mother nucleus with respect to their chromosomes. Moreover, since the somatic nuclei are all alike (except for mutations) in their chromosomal complements, each of them contains characters present in the first nucleus of the series.

VAN BENEDEN (1883) and others came to the conclusion that the individuality of the chromosomes is retained throughout the metabolic stage. ROSENBERG (1909) and NAWASCHIN (1915) confirmed the conclusion for plant cells. BOVERI, VAN BENEDEN, and STRASBURGER also determined that the number of chromosomes in any given species is constant.

The individuality of chromosomes was demonstrated (1930) by BABCOCK in the genus *Crepis* and further emphasized (1937) by GUILLIERMOND who showed that the chromosome or prochromosome is a permanent unit, though its shape may change as the resting stage gives way to the mitotic stage.

The discovery of these important facts established the law of genetic continuity and opened the door to a multitude of new discoveries in the field of heredity. It is true that the idea was not entirely new, for ERNST HAECKEL had announced in 1866 the hypothesis that the cell nucleus is the principal organ of inheritance. But it is doubtful whether anyone of HAECKEL's time foresaw just how decisively the question was to be settled by the cytologists.

The next important question solved was one relating to the changes in the nuclear constitution of cells which conjugate in the process of fertilization. STRASBURGER established the fact in 1888 that nuclei of the germ cells of angiosperms have a reducing division, as a result of which each gametophyte nucleus has half the number of chromosomes possessed by the sporophyte nucleus. The reduction occurs both in the mother cells of the pollen and of the embryo sacs. GUIGNARD also noted this phenomenon in *Lilium* and in the pollen mother cell of *Ceratozamia.* STRASBURGER proved (1893) that a similar reduction also occurs in mosses and ferns. It is interesting to note, incidentally, that the slides of *Osmunda* used in this work were among the first paraffin sections made by STRASBURGER. FARMER and MOORE, who investigated (1905) reduction divisions in animals and plants, applied the term "meiosis", which has since been widely adopted. The terms haploid and diploid have also been generally applied, the first to the reduced number of chromosomes in the gametophytic generation, the second to the number in the sporophytic generation.

Abnormal numbers of chromosomes were discovered as the result of extended investigations of the constitution of somatic nuclei. In these cases it is usually possible to find multiples of the haploid number and this anomalous polyploid condition of the nuclear constitution is frequently associated with anomalous growth of the plant. Gigantism is frequently associated with tetraploidy.

Miss LUTZ found (1912) triploid ($3n$) plants of *Oenothera* which showed great variation, and in the same year DIGBY discovered that *Primula kewensis* is a tetraploid ($4n$). The skillful work of TÄCKHOLM showed (1920) that several species and hybrids of roses are tetraploids and that others are triploids. DE MOL reported (1921) that many of the hyacinths in cultivation are triploids which, on account of the vegetative process of reproduction, can be perpetuated. LESLEY and MANN described (1925) a

case of triploidy in tomato associated with enlargement of leaves and petioles and with partial sterility of pollen. LESLEY has also shown that trisomic types of tomatoes differ in rate of growth and in fruit forming characters from the normal. NAWASCHIN found (1925 and 1927) *Crepis* species with 3, 4, and 5 times the normal numbers of chromosomes.

Heteroploidy of the nuclei has also been found. TÄCKHOLM discovered (1922) forms having more or less than the euploid number of chromosomes, *e.g.* $(2n - 1)$, $(2n + 1)$ or $(4n + 1)$. This condition is designated aneuploidy. CLAUSEN and GOODSPEED found (1924) a trisomic character "enlarged" in *Nicotiana tabacum* which is due to the presence of an extra chromosome. BLAKESLEE and BELLING have analyzed the condition in mutants of *Datura*. The loss of a chromosome seems to cause greater alteration in the behavior of a plant than the gain of one.

The results of numerous experiments show that triploid, tetraploid, and octoploid plants differ slightly from the diploid type (except in size). On the other hand the gain or loss of one or two chromosomes or of the addition of a pair produces far greater effects on the characters of the individual organism. The work of recent years has shown the importance of genetical work in conjunction with cytological investigations.

ROUX and WEISMANN believed that the inheritance units are arranged in serial order along the chromosome. Subsequent research has shown that the chromosome has a longitudinally differentiated structure, though it is not always possible to relate this differentiation very closely to the apparent functional differentiations. Crossing over has been inferred (a) from the structure of bivalents seen at meiosis and (b) from the proportions of different types of progeny found in breeding experiments. In 1892 RÜCKERT suggested that paired chromosomes came together at various points along their length and there exchanged materials. Although ignored for a time, it is now realized that he was essentially correct. In 1909 JANSSENS suggested that the paired chromosomes broke and rejoined at meiosis and that the chiasmata, whose structure was not then clearly understood were the result of this recombination. In the light of this theory MORGAN (1911) was able to put forward the explanation of linkage now accepted.

The theory of the gene has been introduced (1926) by MORGAN and his associates as a means of analyzing the constitution and architecture of the hereditary material. It gives a means of investigating problems of genetics on a numerical basis with a satisfactory degree of accuracy. MORGAN outlined the theory as follows:

> "The theory states that the characters of the individual are referable to paired elements (genes) in the germinal material that are held together in a definite number of linkage groups; it states that the members of each pair of genes separate when the germ-cells mature in accordance with MENDEL's first law; and in consequence each germ-cell comes to contain one set only; it states that the members belonging to different linkage groups assort independently in accordance with MENDEL's second law; it states that an orderly interchange - crossing over - also takes place, at times, between the elements in corresponding linkage groups; and it states that the frequency of crossing-over furnishes evidence of the linear order of the elements in each linkage group and of the relative position of the elements with respect to each other".

MORGAN and his associates and BLAKESLEE have made extensive genetical researches on the basis of the above theory, showing that it is not only plausible but useful. Discrete units of the nature of genes cannot be observed with the microscope. MORGAN suggested that they are of the order of magnitude of certain protein molecules. Evidence of their existence has been chiefly obtained from experimental genetics.

Syngamy:- The union of gametes to produce a fertilized cell is of course essential to the process of sexual reproduction. In the foregoing pages the reader has been made aware of the discovery of important cytological processes in the development of the sexual cells. It is now appropriate to indicate some of the discoveries which led to our knowledge of syngamy, or fertilization in plants.

The first demonstration of a union of two masses of living substance at fertilization resulted from a study of a group of plants, the algae, in which sexuality had not been proved or generally admitted, although suggested by HEDWIG, UNGER, and VAUCHER. The algae were advantageous for the study of fertilization, since the development and behavior of the reproductive organs and cells could, without elaborate preparation, be readily seen under the microscope and often with living material. THURET in 1853, for the first time, saw the active sperm unite with the egg of *Fucus,* and in 1854 proved experimentally that only eggs to which spermatozoids have had access will germinate. FARMER and WILLIAMS (1896, 1898) completed the study of the phenomena to be observed in the living material of *Fucus.* PRINGSHEIM in 1856 watched the spermatozoids of *Oedogonium* push into the receptive tips of the living eggs and saw the characteristic oospore wall formed in consequence. Such a union of the protoplasmic masses of the two sexual cells was soon shown to be a characteristic feature of fertilization in a number of algae, thus, DE BARY saw it in *Spirogyra* (1858) and PRINGSHEIM (1869) repeatedly observed the gradual fusion of the motile gametes of *Pandorina.* It was nearly thirty years later, however, that this phase of fertilization was first seen in seed plants by GOROSCHANKIN and STRASBURGER.

The brown algae were studied, after the time of THURET, by FARMER and WILLIAMS (1896), and by STRASBURGER (1897), both of whom found that the reduction of chromosomes occurred in the first division of the egg and sperm-producing organs, a point where it occurs in no other green plants. STRASBURGER (1906) and YAMANOUCHI (1909) followed out the trend of the chromosome development in other algae. YAMANOUCHI concluded that the *Fucus* plant with its $2n$ number of chromosomes is the sporophyte and that the reproductive organs arising in its conceptacles are sporangia, comparable with those of a seed plant. After the reduction, each of the four megaspores, without escaping, gives rise to a gametophyte of two fertile cells or eggs. Each of the four microspores, in turn, forms a gametophyte of sixteen cells, each of which is fertile and forms a spermatozoid.

The fundamental facts concerning reproduction in the fungi were discovered coincidentally with the overthrow of the belief in spontaneous generation. The splendid work of the brothers TULASNE on the smuts and rusts and their discovery of the oogonium of *Peronospora* in the years from 1847 to 1854 was followed

by the observations of PRINGSHEIM (1857) on the development of zoosporangia and oogonia in *Saprolegnia.* ANTON DE BARY, of whom more will be said in another chapter, corrected certain errors made by PRINGSHEIM and then proceeded to elucidate (1861) the processes of reproduction in *Peronospora.* The work of DE BARY and his numerous students established the fact that the content of an oogonium is fertilized by the escape into it of the living content of the antheridial tube that grows beside it.

BREFELD consistently refused to accept the conclusions of DE BARY that there was any method of sexual reproduction in the ascomycetes. The earliest cytological work on the ascomycetes after the detection of their nuclei by SCHMITZ was that of DANGEARD (1894). He described and figured a fusion of two nuclei in the ascus of *Exoascus* and of *Peziza.* The next year, HARPER, working in STRASBURGER's famous laboratory at Bonn, also described a nuclear fusion in the sexual organs of the hop mildew, *Sphaerotheca.* The whole behavior of the antheridium and the oogonium and their contents had the significance of a real sexual process, as DE BARY had asserted in 1863 and in contradiction to what BREFELD had maintained.

It was not long until HARPER and others described a sexual fusion of the same type in several other of the ascomycetes. Eventually, HARPER determined that there is in these fungi an alternation of a haploid generation (represented by the vegetative mycelium) and a diploid generation (the fertilized oogonium and the ascus-forming hyphae arising from it). The "second fusion in the ascus was regarded as a nutritive phenomenon, to provide a nucleus adequate in size for the organization of the relatively large ascus".

Through the years many workers studied the problem of syngamy in the ascomycetes, but detailed accounts of their work cannot be discussed here. Eventually it was found that fusions of the cytoplasm of sexual cells without caryogamy occur in the higher ascomycetes and basidiomycetes. This fusion results in the formation of a zygote containing both the male and female nuclei (the dikaryon). Caryogamy just precedes the reduction division.

GUILLIERMOND recognized (1940) that the sexual act may occur at a different phase of the life cycle according to the fungus concerned. In yeasts such as *Saccharomyces Ludwigii* caryogamy occurs at conjugation; but that is not true for other yeasts, as *S. ellipsoideus,* where the two haploid nuclei coexist within the zygote and show conjugate division at germination. GUILLIERMOND thus demonstrated by his cytological work that DE BARY and HANSEN had been correct in placing the yeasts among the lower ascomycetes next to the *Exoascales.*

Until toward the end of the last century the basidiomycetes were assumed to be nonsexual fungi; at least no sexual organs had been described for them, with the exception of the spermagonia and aecidia of the plant rusts. The recent work by CRAIGIE on the heterothallic nature of the spermatia will be discussed in the chapter on mycology. When ROSEN discovered in 1892 two nuclei in the aecidiospore of certain species, DANGEARD and SAPPIN-TROUFFY reported (1893) the occurrence of a nuclear fusion in the teleutospore. The latter found (1896) that the cells of the

aecidium-bearing mycelium are uninucleate up to the very base of the chain of aecidiospores. MAIRE first stated clearly (1900) the whole nuclear cycle in rusts, demonstrating a real alternation of generations: the gametophyte or n-generation beginning with the sporidium, the sporophyte or 2n-generation with the mother-cell of the aecidiospore chain. The origin of the binucleate condition of the mother-cell in *Phragmidium* was discovered by BLACKMAN (1904) and CHRISMAN (1905). The time and mode of association of the fusing nuclei, or of their progenitors, are very different in different forms. The fusion and what appears to be the reduction division are, however, constant in location in each species and are always closely associated. In the mushroom, according to WAGER (1893), DANGEARD (1894), HARPER (1902), NICHOLS (1904), and LEVINE (1913), the fusion of nuclei occurs in the basidium, and the reduction at the very next division of this fusion-production when the four spore nuclei are formed.

One of the results of the magnificent work of HOFMEISTER was the discovery of this regular alternation of a sexual and an asexual generation, not only in the life history of the mosses and ferns, but also in that of the seed plants. Since HOFMEISTER's day, detailed investigations by many workers have shown the essential homology, not only of the spore-producing organs and the one or two kinds of spores produced in them, but also of the structures arising from these spores throughout all cormophytes, from the mosses upward.

The fact that the sexual cells of the higher plants are produced on a plant body, or individual, distinct from that which forms the asexual reproductive cells, and that in the normal life cycle the one type of individual arises from and later gives rise to individuals of the other type must be regarded as one of the most significant features of the evolution of plants yet discovered.

The gymnosperms, because of their large eggs, pollen tubes, and nuclei were suitable objects for study. The salient facts of the alternation of generations in higher plants were established in this group. GOROSCHANKIN was able to demonstrate (1883) that in *Pinus pumilio,* the pollen tube opens at the end, and that through this pore the two male cells pass bodily into the egg. GOROSCHANKIN's mistake in supposing both male nuclei to fuse with the egg nucleus was corrected by STRASBURGER the following year. The latter, in 1884, also saw the exit of both male nuclei from the open pollen tube of *Picea,* but found only one male nucleus fusing with that of the egg. In the same publication STRASBURGER also recorded numerous instances in which he had been able to observe the same mode of escape of the contents of the pollen tubes into the embryo sacs in angiosperms. STRASBURGER said, "The most important morphological facts are clear. It is established that the male nucleus that copulates with the egg nucleus passes as such out of the pollen tube into the egg". The development of motile spermatozoids in *Cycas, Ginkgo,* and *Zamia* indicates that these gymnosperms have a close phylogenetic relationship with the pteridophytes. IKENO published (1901) an account of the fertilization process in *Ginkgo* showing that only one spermatozoid fused with the egg cell. WEBBER described (1897 and 1901) the development of the ciliated spermatozoids and the process of syngamy in *Zamia.*

Fertilization by the union of two nuclei in the angiosperms was not readily observed by the earlier cytologists, neither was the entire course of events discovered for some time. GIAMBATTISTA AMICI (1786-1863), a Florentine astronomer and microscopist, noted (1823) the extrusion of the pollen tube from the pollen grain and, in 1830, followed its growth from the stigma through the micropyle to the ovule of *Portulaca.* BRONGNIART (1826) and ROBERT BROWN (1831) also observed the process of fecundation by the pollen tube. Although BROWN traced pollen tubes from the pollen grain into the ovary and into the micropyle of the ovule, he was unable to decide whether, in all cases, any substances passed from the pollen to the interior of the ovule thereby causing the formation of an embryo. He described the change that follows impregnation and the gradual appearance of the embryo. The erroneous views of SCHLEIDEN and of his student, SCHACHT, held up the matter for a time. These men believed that the embryo grew from the lower end of the pollen tube, the ovule merely being a nutrient contrivance. AMICI finally set the matter right. The epoch-making publication in 1761 by KOELREUTER in which he correctly described the process of pollination in flowering plants thus was followed, after the lapse of more than a century, by an understanding of the gametic fusion which followed pollination. STRASBURGER first demonstrated that the generative nucleus, carried at the end of the pollen tube, enters the embryo sac and unites with the egg nucleus. The fact has been abundantly supported by a host of other cytologists. STRASBURGER and GUIGNARD thought that only one of the generative nuclei entered the embryo sac, but later GUIGNARD and NAWASCHIN discovered that both generative nuclei entered the embryo sac. One of these unites with the egg-nucleus and thus effects fertilization. The other unites with one of the polar nuclei (usually the upper), which then unites with the other polar nucleus. The embryo arises from the fertilized egg cell, and the nucellus, which serves for the nutrition of the embryo, from the triploid nucleus.

It remained for the cytologists, therefore, in the closing years of the 19th century to solve one of the problems of sexual reproduction which had been raised by Assyrians at the dawn of history. The solution of the problem waited many centuries for lack of knowledge of the cell and of techniques for its study. The intricate structure of the nuclei and its role in inheritance have already been surveyed.

Plastids:- The varied forms and arrangement of chloroplasts intrigued microscopists at an early date. The circulation of plastids in cells of *Chara* had been noticed some time prior to the discovery of protoplasm, in fact, for a time it was thought that they swam in the cell sap instead of being carried in the cytoplasm.

VON MOHL was very clear in his statements that chlorophyll is contained only in the plastids; they have a characteristic organization, they have a globular form in the majority of plants, though in the algae they may have a band structure. He extracted the green pigment from plastids and saw that the substratum had been little altered in size. The application of iodine to cells from which the color had been extracted stained the plasts yellow, from which he thought it probable that they were protein compounds.

PRINGSHEIM gave (1879) the name "stroma" to the substratum of the plastid. SPRENGEL, MEYEN, AGARDH, and others made the assumption that the plastids have an utricular structure, but VON MOHL was unable to discover the alleged enveloping membrane distinct from the contents.

The chemist MULDER analysed chlorophyll, obtaining the formula $C_{18}H_{18}N_2O_3$ and assumed that it was allied to indigo-like bodies. He conjectured that uncolored chlorophyll exists in all parts of the plant, capable of conversion into green by free oxygen. VON MOHL was unable to accept such a theory, stating that, whatever its nature, it was always intimately associated with plastids, even at its first appearance in etiolated plants. VON MOHL distinguished between chlorophyll and the red and blue pigments dissolved in the cell sap, noting, however, that in some cases organized chromatophores were present. KÜTZING discovered that in some red algae the chlorophyll in the plastid is masked by red pigments. VAUCHER first described (1803) pyrenoids in plastids of algae, and SCHMITZ carefully investigated them, giving them in 1882 the name they bear. The motile cells of the lower plants, *e.g.*, zoospores and gametes, frequently contain pigmented structures called "eyespots". STRASBURGER showed (1900) that they may arise as a swelling of the ectoplast. In the zoospore of *Cladophora* he found an external pigmented layer superposed on a colorless, lens-shaped structure. The eyespot in the spermatozoid of *Fucus* was reported by GUIGNARD (1889) to arise from a plastid in the antheridial cell, although OVERTON concluded (1889) that it was formed *de novo* in each young zoospore of the green algae he studied. SHARP summed up the evidence (1926) concluding that in many cases the structure and function of this problematical body closely resemble the ordinary plastid, but in other cases it appears to represent a differentiation of the ectoplast.

The almost invariable association of starch with plastids was apparent from the beginning of cytological studies but its true relationship was not apprehended until a later time. It was frequently said that chloroplasts could be transformed into starch grains and *vice versa*. The cytologists saw starch grains appear within chloroplasts under certain conditions, yet there was a prevalent belief until 1880 that there could be a free formation of starch grains either in the cell sap or in the protoplasm, because men could sometimes see them in chlorophyll-free cells. Then it was SCHIMPER who in 1880 and 1885 proved that starch is not formed except in a plastid of some sort, be it colorless or colored. SCHIMPER and STRASBURGER gave us the names leuco-, chloro-, and chromoplasts and clearly expounded their physiological differences. The progress of knowledge of the genesis of starch will be given in a subsequent chapter.

PRINGSHEIM announced (1874) and MEYER concurred (1883) that the stroma of the plastid has a spongy structure whose cavities hold the green coloring matter. A stratification of the pigment was announced (1903) by TIMIRIAZEFF after some skillful work on the plastids of *Phajus*. He concluded that the green pigment formed a very thin layer on the surface of the plastid. The structure of the plastid has been recently reinvestigated by ZIRKLE (1926 and 1927) who believes that the chloroplasts of *Elodea* and *Selaginella* are hollow, flattened ellipsoids with a central vacuole

which may contain one or more grains of starch. Modern investigators have returned to the concepts of the earlier workers. They conclude that the pigment is held in the form of discontinuous "grana" in the stroma of the plastid.

MÖBIUS directed attention (1920) to the relative constancy in size of the chloroplasts of higher plants. The significant differences in the size of chloroplasts in certain genotypes of maize was determined (1929) by EYSTER. He found that although the size in most types varied from 6 to 7μ. or from 7 to 8μ. in their length, others had plastids which ranged from 10 to 25μ. in their longest dimensions. EYSTER concluded that the size of plastids in maize was a heritable character. He reported also an inverse relationship between the size and total number of plastids in a cell.

The question of the origin of the plastids has waited long for a complete answer. NÄGELI saw (1846) the direct division by elongation and constriction of chloroplastids in algae. SANIO made the first observations (1864) on the divisions of plastids in angiosperms (see Bot. Zeit. 22:193). SCHMITZ concluded (1882) that the plastids of algae were never formed *de novo,* but arose from the division of pre-existing plastids. SCHIMPER concurred in the idea and added that in angiosperms they were originally derived from the meristem. ALLEN studied (1905) the division process in *Coleochaete,* in which each cell and gamete has one nucleus and one plastid. He reported that after the sexual union of the gametes the zygote contains one nucleus and two plastids. These two plastids divide at the first division of the zygote, but not at the second, the resulting four cells consequently had one plastid each.

In the ontogeny of the higher plants there remained the problem of plastid development from the gametes or at any rate from the embryo plant in the sexual, and from the meristems in asexual reproduction.

The assumption of SCHIMPER and MEYER that undifferentiated plastids multiply by division and are handed down from generation to generation rested on incomplete evidence, because no one had ever demonstrated the presence of these plastids in the egg cell. The question of plastid origin was thrown open again by the discovery (1897) by BENDA of the mitochondria (often called chondriosomes). These organs have the shapes of small granules, rods, or threads and are almost universally present in cytoplasm.

LEVITSKY (1910-1913) and GUILLIERMOND (1911 and later) concluded that the leuco-, chloro- and chromoplasts in flowering plants develop from mitochondria which arise in turn from the divisions of pre-existing mitochondria in the embryonic tissues. LEVITSKY (1910-13) and GUILLIERMOND (1910-19) demonstrated that the plasts evolved from chondriosomes of the embryonic cells. The former believed that the chondriosomes arose *de novo* from the cytoplasm; the latter, that they were permanent organs, transmitted from cell to cell at the time division occurs. GUILLIERMOND'S experimental results support the views of SCHIMPER and MEYER in showing that the plasts differentiate from elements which are ever present in the cell, be it animal or plant, and are transmitted from cell to cell.

EDSON'S discussion (1915) pointed out the cytological and genetical importance of mitochondria. The migration of mitochondria

at the same time with the nucleus from the antheridium at the time of fertilization invited speculation as to their function.

This confirmation of the older ideas of SCHIMPER and MEYER was not allowed to go unchallenged. Some writers refused to admit that anything remained to be discovered about the origin of plastids, others considered the alleged structures to be artefacts produced by physico-chemical changes in the cell constituents.

The situation was somewhat confused by the ideas of a group of investigators who attempted to reconcile the divergent ideas above stated. MOTTIER, for example, who found mitochondria (1918) in all cells of the *Marchantia* thallus, however, maintained that they differed, from plastid primordia. He concluded that leucoplasts and chloroplasts are derived from granular or rod shaped primordia which are permanent organs of the cell with the same rank as the nucleus. These primordia were said to multiply by division. Full grown chloroplasts also multiply by division. He recognized also other granular and rod shaped bodies which do not give rise to either chloroplasts or leucoplasts and to which the name mitochondria is restricted. These mitochondria multiply by division and are permanent organs of the cell. He confirmed LEVITSKY's and GUILLIERMOND's results, but held, without proof, that mitochondria and plasts are essentially different. RUDOLPH also concluded (1923) that there are two distinct types of primorida in meristematic cells, notwithstanding a morphological and histochemical similarity which renders their distinction impossible, namely mitochondria and young plastids. The first retain in the growing cell their appearance and their histochemical reactions; the second develop into leuco-, chloro-, or chromoplasts. RUDOLPH's idea was supported by SAPĚHIN, SCHERRER and MOTTIER. They believed that the embryonic cells of phanerogams should contain tiny plasts actively dividing, showing the same aspect as mitochondria, and only distinguishable from the latter after they differentiate. They affirmed that plasts had nothing in common with mitochondria which they regarded as nothing more than metabolic products. LEVITSKY and others have been unable, however, to verify the idea that the mitochondria and the plastid primordia were different. TWISS, in a very conservative discussion of his results on *Preissia* and *Zea* cells, opines that there can be no question of the existence of mitochondria, nor that they are normal constituents of cytoplasm. He was uncertain about the evidence for the division of mitochondria and for their functions in heredity.

The difficulty of the problem is enhanced by the fact that the organs are so small as to approach the lower limit of microscopic visibility. RANDOLPH was unable to discover (1922) the origin of what he called protoplastids, concluding that the smallest of the particles were sub-microscopic in size. He found only one type of granule. He concluded "The presence of these transitional stages within a single cell furnishes convincing proof of the origin of chloroplasts from bodies which at first are scarcely visible, and which one is led to believe may even arise *de novo* from the cytoplasm".

The question of plastid origin is regarded by most cytologists as unsettled, though great advances have been made. SHARP remarked (1926) that cytologists have probably underestimated the

capacity of protoplasm for epigenetic differentiation. If one assumes that plastids represent regional transformations of the cytoplasm resulting from the localization of certain processes, they may be expected to differentiate anew as these processes begin, and to preserve varying degrees of permanence depending on the processes involved.

The problem of plastid differentiation was solved by the researches of GUILLIERMOND and his students MANGENOT and EMBERGER (1920-24) who demonstrated:-

(1) Chloroplasts and mitochondria exist *pari passu* in the vegetative and reproductive stages of algae and certain bryophytes. Each of these arises from divisions of pre-existing chloroplasts or of mitochondria, respectively, without evidence of transformations of one into the other.

(2) Embryonic cells of phanerogams contain chondriosomes which look exactly like those of animal cells; among these chondriosomes *a part* differentiate into the plasts of the green cells, *others* remain as chondriosomes; among the chondriosomes in the embryonic cells it is generally impossible to designate those which will differentiate into plastids.

(3) Cells which never become green contain leucoplasts which retain the shape of chondriosomes and can only be known by their starch-forming ability.

(4) It is only in the green cell that a plastid can really be distinguished from a chondriosome.

(5) Chondriosomes as well as plasts are permanent elements, to be transmitted at all divisions.

Studying living epidermal cells of monocotyledons, GUILLIERMOND observed that leucoplasts and chondriosomes show the same aspect, and the same feeble refringency. Both consist of a plastic, semifluid substance, slowly shifted and distorted by cytoplasmic currents; both are very fragile, easily converted into large vesicles; both stain in the living cell by Janus Green, methyl violet, dahlia, and other stains. Both bodies are made up of a complex of lipoproteins with lipids (lecithin) which explains why they are destroyed by ordinary killing fluids. Both react similarly toward microchemical reagents: therefore plastids behave in all respects as chondriosomes.

Fern sporangia develop from epidermal cells which contain big chloroplasts *and* small chondriosomes; in microsporidial cells EMBERGER observed that chloroplasts lose their chlorophyll and revert to tiny elements like chondriosomes. As spores germinate some chondriosomes differentiate into chloroplasts. Cells of prothallia which will become sexual cells show a similar regression of chloroplasts into non-chlorophyll bearing rod shaped elements, the *ensemble* forming a homogeneous chondriome which, as the egg develops and tissues differentiate, shows the same evolution as was described above for phanerogams. Structures which appear like chondriosomes obtained thus from the dedifferentiation of plastids may again yield plastids. Indeed, among the *Selaginellae* the cell shows a single plast differentiated from a structure appearing like the other chondriosomes, though noticeably larger, and therefore easy to detect in any embryonic cell. MANGENOT discovered similar features among the higher algae; the chloroplasts (rhodoplasts) of the *Florideae* lose their pigments in sexual cells and there dediffer-

entiate into chondriosome-like bodies, later to differentiate again into colored plastids.

The researches carried on by GUILLIERMOND and his students demonstrated the existence of two categories of permanent elements which are transmitted from cell to cell at division:— (a) the chondriosomes which exist either in plant or animal cells, and (b) plastids which exist only in green plants. GUILLIERMOND concluded that plastids belong to a special category of chondriosomes in that they are connected with photosynthesis in green plants and that both are closely akin, being permanent organs in the cell, resembling each other.

Vacuoles:- When the early cytologists turned their lenses on plant cells, they saw that the living organized protoplasmic structures filled only a part of the space bounded by the cell wall. The discovery of the vacuole by SPALLANZANI led to no true conception either of the vacuole or of the cell. MEYEN (1835 and 1838) and SCHLEIDEN (1842) and others clearly distinguished between cytoplasm and vacuoles.

HOFMEISTER (1867) recognized DUTROCHET's explanation (1828) of water intake by endosmosis, and formulated the concept of turgidity resulting from the flow of water into the vacuole. HOFMEISTER explained the origin of vacuoles very simply on the assumption that when the amount of water in protoplasm exceeded a certain ratio, the excess was excreted in droplets into the interior of the protoplasmic mass where it assumed the forms of sharply defined spherical vacuoles, which, by continual volume increases, broke down the thin intermediate partitions of protoplasm and eventually formed a single large vacuole. The importance of the interface between the aqueous contents of the vacuole and the surrounding cytoplasm was recognized and properly emphasized by DE VRIES. Recent work by CHAMBERS and others showed that the membrane is tough, elastic, and sticky, apparently having properties not possessed by the remaining cytoplasm. LLOYD and SCARTH have shown (1926) that it has many of the physical properties of lecithin and that it is, in a measure, independent of the life of the cell.

A true appreciation of the nature of the vacuole was not afforded until the works of DE VRIES and PFEFFER were published. The former established that the vacuolar sap is something not only distinct from the cytoplasm, but essential for the functioning of the cell. He interpreted anew the concept of turgidity imposed by the endosmotic flow of water into the vacuolar solution.

PFEFFER gained (1886) further information on the phenomenon of the vacuole through his investigations on the absorption of certain anilin dyes by living cells. Having found by experience that methylene blue and other stains exerted no toxic action at great dilutions, he investigated the processes of absorption with the so-called Vital Dyes. He discerned that the amounts of methylene blue absorbed by the cytoplasmic envelope were comparatively small, contrariwise, the dye accumulated in the vacuolar sap, eventually coloring it more deeply than the external solution. The absorption of other dyes by the cytoplasmic layer did not, however, hinder their penetration into the vacuolar sap. PFEFFER was one of the first to notice that the absorbable anilin dyes can

give important data on the reaction of protoplasm and of vacuolar sap, showing the topography of vacuoles and clearing away many vague conceptions.

A great interest in the absorption of Vital Dyes was eventually developed, and many important phenomena have been learned by this technique. GUILLIERMOND and GAUTHERET discovered (1937) that there is a certain amount of reversibility in the absorption of Vital Dyes by yeast cells. They found that the dyes absorbed by the cytoplasm were actively transferred to the cell vacuole, sometimes as the leuco form, which was reoxidized to the original dye in the vacuole. Subsequently it may be reabsorbed by the cytoplasm and transferred again to the external medium. GUILLIERMOND concluded (1938) that both the basal vital dyes and their leuco-derivatives are accumulated in the vacuoles of living cells, but they penetrate more slowly than the oxidized forms. Frequently the leuco-derivatives have the same properties in relation to the cells as the corresponding dyes, but it does not always occur.

A correct understanding of the origin of the vacuole was not easily obtained and there is at present no complete unanimity of opinion on the subject. PFEFFER and DE VRIES recognized that the small discrete vacuoles present in meristematic cells coalesced, as growth and differentiation proceeded, thereby forming a single large vacuole. DE VRIES opposed (1885) the idea that vacuoles arise *de novo,* stating that they arise from primordia which he called tonoplasts. The tonoplasts were conceived to be definite organized structures which arose from the division of preëxisting tonoplasts. VAN TIEGHEM endorsed (1889) this opinion, but named the primordia hydroleucites. WENT formulated (1888) a somewhat different concept of the origin of the vacuole. Having found extremely small vacuoles in the reproductive cells of algae and in meristematic cells of the higher plants, he discarded the idea of a tonoplast in favor of the idea that all vacuoles arise from preexisting vacuoles. As a result of the questionable technique which DE VRIES and WENT employed, adverse criticism was levelled at their conclusions and the older concept of HOFMEISTER was reestablished. BENSLEY formulated (1910) the new concept of the vacuome. He described in young cells a very delicate network which, as the cell ages, enlarges and forms the large vacuole of the mature cell and believed that the network of canals is homologous with Golgi bodies.

DANGEARD (1916) observed vacuoles to appear first as tiny, isolated, bead-like grains, or as threads which fuse more or less into a network. GUILLIERMOND showed that the vacuome is distinctly different from the chondriome. Each absorbs different dyes. The colloidal substances in the vacuoles of flowering plants differ widely in different cases; often the vacuolar contents are composed of alcohol-soluble protein, mixed with phenol compounds of the tannin group and closely related anthocyanin compounds. According to its hydration, the vacuome can therefore show one of these three alternate aspects: (1) solid, round, small bodies; (2) a mitochondria-like network of thick paste; (3) large, round, ordinary liquid vacuoles. In the solid phase the vacuome does not stain with intra-vitam dyes; in the liquid stage it stains faintly, since part of its colloids are thrown down in the form of deeply stained granules.

CHARLES DARWIN made (1875) important observations on the vacuoles of the cells of the tentacles of *Drosera,* especially with respect to the effects of stimuli on the forms of the vacuoles. The sap of those cells contains a purple pigment which enabled DARWIN to see the changes in shape of the vacuole. The colored sap was uniformly distributed in the unstimulated cells due to the parietal position of the colorless protoplasmic material and the unity of the central vacuole. He made a point of the circulation of the cytoplasm around the vacuoles. The cogency of his descrip-

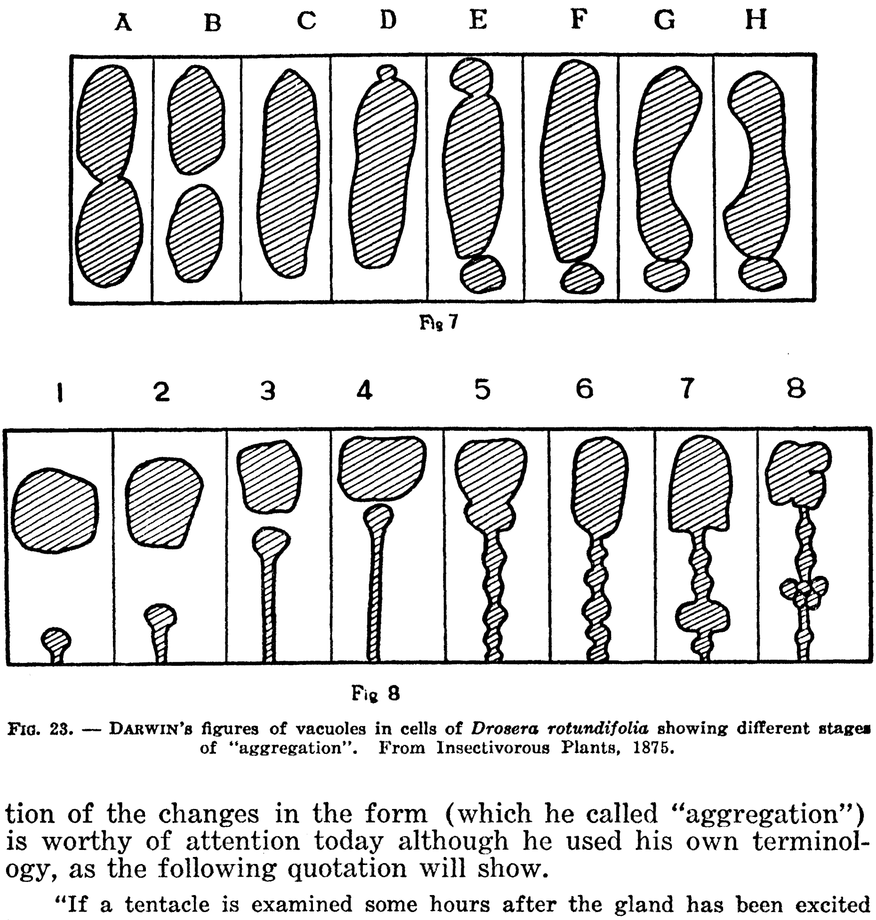


FIG. 23. — DARWIN'S figures of vacuoles in cells of *Drosera rotundifolia* showing different stages of "aggregation". From Insectivorous Plants, 1875.

tion of the changes in the form (which he called "aggregation") is worthy of attention today although he used his own terminology, as the following quotation will show.

"If a tentacle is examined some hours after the gland has been excited by repeated touches, or by an inorganic or organic particle placed upon it, or by the absorption of certain fluids, it presents a wholly changed appearance. The cells, instead of being filled with homogeneous purple fluid, now contain variously shaped masses of purple matter, suspended in a colourless or almost colourless fluid. The change is so conspicuous that it is visible through a weak lens, and even sometimes by the naked eye; the tentacles now have a mottled appearance, so that one thus affected can be picked out with ease from all the others. The same result follows if the glands on the disc are irritated in any manner so that the exterior tentacles become inflected; for their contents will then be found in an aggregated condition, although their glands have not as yet touched any object. But aggregation may occur independently of inflection, as we shall presently see. By whatever cause the

process may have been excited, it commences within the glands, and then travels down the tentacles. It can be observed much more distinctly in the upper cells of the pedicels than within the glands, as these are somewhat opaque. Shortly after the tentacles have re-expanded, the little masses of protoplasm are all redissolved, and the purple fluid within the cells becomes as homogeneous and transparent as it was at first. The process of redissolution travels upwards from the bases of the tentacles to the glands, and therefore in a reversed direction to that of aggregation." . . .

"The little masses of aggregated matter are of the most diversified shapes, often spherical or oval, sometimes much elongated, or quite irregular with thread or necklace-like or club-formed projections. They consist of thick, apparently viscid matter, which in the exterior tentacles is of a purplish, and in the short discal tentacles of a greenish, colour. These little masses incessantly change their forms and positions, being never at rest . . . If their shapes are sketched at intervals of a few minutes, they are invariably seen to have undergone great changes of form; and the same cell has been observed for several hours. Eight rude, though accurate sketches of the same cell, made at intervals of between 2 m. or 3 m., are here given (fig. 7), and illustrate some of the simpler and commonest changes . . .

"The cell above figured was from a tentacle of a dark red leaf, which had caught a small moth, and was examined under water. As I at first thought that the movements of the masses might be due to the absorption of water, I placed a fly on a leaf, and when after 18 hrs. all the tentacles were well inflected, these were examined without being immersed in water. The cell here represented (fig. 8) was from this leaf, being sketched eight times in the course of 15 m. These sketches exhibit some of the more remarkable changes which the protoplasm undergoes. At first, there was at the base of the cell 1, a little mass on a short footstalk, and a larger mass near the upper end, and these seemed quite separate. Nevertheless, they may have been connected by a fine and invisible thread of protoplasm, for on two other occasions, whilst one mass was rapidly increasing, and another in the same cell rapidly decreasing, I was able by varying the light and using a high power, to detect a connecting thread of extreme tenuity, which evidently served as the channel of communication between the two. On the other hand, such connecting threads are sometimes seen to break, and their extremities then quickly become club-headed. The other sketches in fig. 8 show the forms successively assumed". (Insectivorous Plants, Chapter III).

The response of the vacuole to cellular derangements has been extensively studied by DUFRÉNOY (1930 and 1935), and the importance of this aspect of cellular pathology clearly demonstrated. Injuries caused by parasitic fungi or by virus disease are generally reflected in the transformation of the large central vacuole into many smaller vacuoles thereby greatly increasing the interfacial surfaces of the vacuolar-cytoplasmic system. Eventually the contents of the vacuoles of affected cells may exhibit discoloration. DUFRÉNOY has successfully applied microchemistry to the study of vacuolar inclusions.

Recapitulation:- The development of knowledge of the cell as the unit structure of organisms has been briefly traced through a century of assiduous study by many investigators. The results obtained in spite of innumerable difficulties have shed a beneficent flood of light on the nature of the organism. The genesis of the organisms and the centers of metabolic activities have been elucidated to a far greater extent than would otherwise have been possible. Not only that, but the marvelous coördinations between cells have explained many of the fundamental processes of growth and differentiation.

REFERENCES:-

BEAUVERIE, J. (1912): Edouard Strasburger. Rev. gen. bot. 24:417, 479.

DUFRÊNOY, J. (1935): Structure et métabolisme cellulaire. Arch. d'Anat. Micr. 31:1-77.

GUILLIERMOND, A. (1929): The recent development of our idea of the vacuome of plant cells. Amer. Jour. Bot. 16:1-22.

—— —— (1940): Sexuality, developmental cycle, and phylogeny of yeasts. Bot. Rev. 6:1-24.

—— —— (1941): Cytoplasm. Chronica Botanica, Waltham, Mass.

GUILLIERMOND, A., MANGENOT, G., et PLANTEFOL, L. (1932): Traité de cytologie végétale. François, Paris.

KARSTEN, G. (1912): Eduard Strasburger. Ber. D. Bot. Gesells. 30:(61)-(86).

KÜSTER, E. (1935): Die Pflanzenzelle. Fischer, Jena. (Bibliography valuable).

MOHL, H. VON (1851): Grundzüge der Anatomie und Physiologie der vegetabilischen Zelle. Vieweg, Braunschweig. (Eng. transl. by HENFREY, 1852, London).

MORGAN, TH. H. (1926): The theory of the gene. Yale University Press, New Haven, Conn.

PFEFFER, W. (1886): Über Aufnahme von Anilinfarben in lebende Zellen. Untersuch. bot. Inst. Tübingen 2:179-332.

SCHLEIDEN, M. J. (1842-3): Grundzüge der wissenschaftlichen Botanik. Leipzig. (Eng. transl. by LANKESTER, 1849, London).

SHARP, L. W. (1926): An introduction to cytology. Second ed. McGraw-Hill, New York. (Bibliography valuable).

TISCHLER, G. (1934): Allgemeine Pflanzenkaryologie. 2te Aufl., Borntraeger, Berlin. (Bibliography valuable).

V[INES], S. H. (1892): Nägeli (obituary note) Proc. Roy. Soc. 51:XXVII-XXXVI.

WILSON, E. B. (1902): The cell in development and inheritance. Second ed., Macmillan, New York.

ZIRKLE, C. (1937): The plant vacuole. Bot. Rev. 3:1-30 (With bibliography).

Chapter XII.

THE WATER ECONOMY OF PLANTS.

Sap ascent:- The dependence of plants on an adequate supply of water had been known from the earliest times, but, aside from MALPIGHI, GREW, and HALES, few had apparently devoted any serious study to the question. At the inception of the 19th century, the old idea prevailed that there was some sort of analogy between the movements of sap in plants and those of blood in animals.

THOMAS ANDREW KNIGHT, a gifted amateur, experimented upon trees and demonstrated ascending and descending currents of sap. Having skillfully removed the bark and cortex, he observed that the buds above the decorticated band developed normally, in contrast to the buds below the band which were completely arrested. He concluded that a stream of descending sap passed through the cortex and that an ascending stream passed through the alburnum, but he did not understand the forces which drove the sap through these layers, as well as did HALES, nor did he perceive any difference in the composition of the two currents.

The subject was investigated and greatly clarified by DUTROCHET who discovered (1826) endosmosis and applied it to the problems of absorption and transfer. In 1828 he introduced the concept of osmosis into physiological response and showed that the movements of plant members are often due to variations in cell turgor which, in turn, are dependent upon osmotic exchanges of fluids. Constructing osmometers similar to those employed in modern physiological laboratories, he recorded the inflow of water against various solutions and concluded that the velocity of the endosmosis produced by various densities of the same inner fluid, is in proportion to the excess of the density of the inner fluid over the density of the water bathing the semi-permeable membrane. DUTROCHET elucidated certain problems about translocation in *Chara* and formulated valuable ideas about the functions of leaves in controlling ascending and descending currents of sap. He may be regarded as the founder of the science of physical biology in relation to plants.

The anatomy and physiology of the woody stem began to be assiduously studied in the first decades of the 19th century, but without immediately making any conspicuous progress. It was difficult to free the mind from the idea of a pumping mechanism in the plant which sent the sap current upwards.

AUGUSTIN P. DE CANDOLLE, a brilliant student and an able botanist, went off on a tangent with his idea of the contractile spongiole at the root tip. His spongiole, which was a root-cap, was said (1832) to have the power of active contraction, by which it could suck up the solution with which it was in contact. He stated that the absorbing force of the spongioles appeared to be due to their vital action, combined with capillarity, and especially with the force of hygroscopic attraction which is characteristic

of plant tissue. He was essentially correct in his ideas of non-selection by the spongioles, noting that they appear to absorb nearly everything found in the soil without regard to the needs of the plant, and he adopted DE SAUSSURE's idea that the plant roots absorb proportionally more water than solute. DE CANDOLLE's belief in his theory was daunted neither by the fact that the ends of excised branches absorb water without the action of the lively spongioles, nor by the observation that disorganized spongioles give a freer passage than the intact to the passage of sap. He was correct in concluding that the leaves draw up the sap and exhale the superabundant water to the atmosphere, thus accounting for the ascent of sap. He thought that the cellular envelope which surrounds the stem, and which communicates with all the layers by means of the medullary rays, draws the sap transversally by the activity of the living cells, and thus resorted to the "vital action" of living cells as a *deus ex machina,* when other explanations failed.

MEYEN, TREVIRANUS, and others who worked on these problems were no more successful than DE CANDOLLE. A few words about their work must suffice. MEYEN's "Neues System der Pflanzenphysiologie" (1837-39) rejected DE CANDOLLE's spongiole theory and adopted DUTROCHET's conclusions on the importance of osmosis for acquiring and translocating fluids in the plants. MEYEN, however, added nothing either essentially new, or of lasting value. He was pretty certain that the salts which are acquired along with the water are essential food constituents, but DE SAUSSURE had discovered that fact and published it in 1804. TREVIRANUS could not relinquish the concept of a vital force which carried the sap to the leaves.

The period from 1800 to 1850 witnessed the birth of a new realistic natural philosophy first in Germany and later in other countries. The concept that living matter exhibits definite physical and chemical properties did much to dispel the esoteric atmosphere which had surrounded botany. While the new goal has not yet been reached, there has been much progress since the outlook changed. HUGO VON MOHL formulated a new and illuminating concept of the absorption of water and dissolved substance. In his book "Die vegetabilische Zelle" he said (1851):

"In all plants the fluid nutriment is taken up by absorption through cells. As the cell membrane has no orifices, only such matters as are actually dissolved, can be absorbed into the cell with the water which penetrates the cell membrane; . . . ". (HENFREY's translation).

The problem of sap movement in the plant was shown by VON MOHL to present far greater difficulties than that of absorption by cells which are in direct contact with the aqueous medium. He wrote further:

"At first sight it seems very easy to give an explanation of the ascent of the sap, both before the opening of the buds at the recommencement of vegetation, as well as during the period in which the plants are clothed with leaves. During the period of the rest of vegetation, the cells of a perennial plant are filled with a great quantity of organic compounds, under the form of proteine substances, sugar, gum, and more particularly of starch, which latter is converted into sugar at the recommencement of vegetation. In consequence of this, the cell-sap becomes capable of setting up a powerful endosmose, and nothing seems more natural than that the cells of the roots should absorb the water which exists around them, and that the sap diluted by this should be taken up by the cells above, and so be carried gradually upwards

from one cell to another, whence the notion that endosmose is the sole and sufficient cause of the motion of the sap, counts many adherents even in recent times. But on closer examination the matter appears less simple than it seemed at the first glance. The organic compounds, especially the starch, are not, for the most part, contained in the elongated cells of the wood, in which the sap ascends, but more particularly in the cells of the medullary rays and in those of the rind of the root, while in those Monocotyledons, which, like the Palms, lay up a store of sugar, gum, starch, etc., before the time of flowering, these substances are deposited in the parenchymatous cells of the stem. Thus the substances which cause the setting up of the endosmose, occur in cells which do not preside over the conveyance of the sap, while in the elongated cells of the wood, substances which would cause endosmose exist only in inconsiderable quantity, and in the vessels not at all. How then does the sap reach the wood-cells and vessels, and how is its motion imparted to it? I consider these questions as unsolved at present" (HENFREY's translation).

VON MOHL attacked the problem with such scientific acumen that his discussion appears essentially modern even after the lapse of nearly a century. The world is indebted to him for the first clear exposition of the rôle of endosmosis in the physiology of the plant.

The next significant advance in the understanding of the acquisition of water by plants was made by SACHS in his discussion of the importance of root hairs. In his "Experimentelle Pflanzenphysiologie", he gave (1865) an enlightening discussion of the relations between root hairs and the water films on soil particles. Commenting on the fact that it is the younger portion of the root which absorbs the principal part of the water, he called attention to the presence of root hairs a short distance back of the growing tip. His ingenious diagrams showed root hairs among soil particles each of which held a thin film of water by surface attraction. The walls of the root hairs being in intimate contact with the aqueous films remove water from the soil particles and deliver it to other cells of the root. SACHS was somewhat hazy in discussing the reasons for the continued movement of water into the root-hair although he was certainly familiar with the phenomenon of endosmosis which VON MOHL had so clearly described.

SACHS was greatly interested in the phenomenon of water movement in plants and cited many examples proving that an upward flow takes place from regions rather remote to the leaves and growing points. The rate of flow upwards, according to SACHS, is naturally dependent upon various external conditions, especially upon those which affect the rate of transpiration. The current of water in the wood which replaces the transpirational loss, said he, cannot be caused by osmosis, since the vacuoles of conducting wood-cells are not filled with sap, but contain air bubbles at the time when the movement is most rapid. In 1874 he announced his conclusion that the water moves in the plant as imbibed water in the tracheal walls without the coöperation of living cells, and not in the cell cavities. SACHS emphasized the idea that the wood consists of a frame work of lignified lamellae which enclose cell cavities. The walls may contain imbibed water, and the amount of their swelling would depend upon the quantity of water absorbed; moreover, they contain no capillaries into which liquid or air could directly penetrate. These water-conducting organs permanently lose their ability to convey water once they

have become air-dry. He admitted that wood, after having been dried, may become saturated with imbibed water, but added that this water no longer possessed mobility. SACHS did not pass lightly over this matter and emphasized that certain unknown internal factors determine the movement of the transpiration current in the wood. He pointed out that the natural alteration which occurs with increasing age and which converts the wood into duramen, or heartwood, also deprives it of the ability to convey imbibitional water. Most of the water moves upward in the alburnum, or sap-wood.

One cannot fail to be impressed by the great weight of the columns of water in tall trees and with the forces which must exist to sustain them. SACHS' imbibition theory would account for such force since it involved intramolecular forces far greater than the pull of gravity, but he realized that it is another question, whether the rapidity of the molecular movements of water of this nature might be sufficiently great to meet the requirements of the transpiring foliage on a hot day. SACHS left the problem of sap translocation in plants without having contributed much to its solution, although his analysis of certain aspects of the problem tended to clarify it. It was not long until ELFVING and VESQUE discounted the idea that the sap currents pass through tracheal walls. When those two investigators plugged the lumina of conducting elements with cacao butter, they found that translocation practically ceased. SACHS had, however, performed a useful service in this field by drawing attention to the physical nature of forces involved in the phenomena of translocation, although he did not give any fundamental explanations of the sap flow.

Attention then swung to vital forces which might cause sap translocation. GODLEWSKI concluded (1884) that the pumping action of living cells was necessary. This action he ascribed to a periodic fluctuation in the permeability of the cytoplasm of parenchymatous cells in the plant stem comparable to the older ideas on pulsations in plants. In woody plants the cells of the medullary rays which are in contact with tracheae were assumed to fill with water and then by a change in the permeability of the plasma membrane, these living cells were thought to force water into the contiguous tracheae. GODLEWSKI assumed that the injected water moved upwards rather than downwards because the air pressure in the tracheal vessels was greater at the base of a plant than in the upper region. He claimed that his theory explained the radial position of the bordered pits, which contributed to the stair-case movement of the water upward in the stem, and also the radial intercellular spaces along medullary rays through which an exchange of gases necessary for the respiration of the living cells might be possible. GODLEWSKI was unable, however, to prove the essential features of this hypothesis. WESTERMAIER and JANSE supported this theory of the essential rôle of living cells but without establishing its validity. Some of JANSE's ideas seem to postulate the existence of a perpetual motion machine.

The inadequacy of these concepts of the importance of living cells in sap movement was shown by the painstaking work of the cytologist, EDUARD STRASBURGER, in his publication "Über den Bau und Verrichtungen der Leitungsbahnen in den Pflanzen" (1891)

which contains an extensive summary of previous studies on the ascent of sap. The descriptions of the anatomy of various groups of plants is of less importance at the moment than his studies on the ascent of liquids in trees and large branches. He made many observations on the rise of liquids, not only in intact trunks, but through portions of trunks in which the living cells had been killed by heat or by poisons.

Time and again STRASBURGER returned to the conclusion that the forces which move the sap upward are physical rather than physiological. He was working at a time when polemical discussions were rife and his painstaking histological studies on the length and diameter of tracheids corrected some prevalent misconceptions. He concluded that the neighboring living cells of the water channels press into them their cell sap. If the channels were already full a hydrostatic pressure would be created. The tracheal channels of the roots withdraw water from the cells adjoining them. These cells in turn absorb it by osmosis from the soil. He obtained evidence from young trees which demonstrated that the vital hypothesis was unnecessary. For example, he found that trunks more than 10 meters high continued to draw up water although the living cells in the base had been killed by exposure to a temperature of 90°C. When the cells at the base of the shoots were killed by strong poisons, among which copper sulfate, alcohol, and picric acid may be mentioned, the results were similar. STRASBURGER sawed off, under water, the trunks of young *Robinia* trees as tall as 11 meters. After the cut base had been retained in water for an hour, one of the trees was transferred to aqueous eosin, whence it absorbed in 24 hours about a liter of the dye solution which reached the apex of the tree and was found not only in the vessels of the wood of that season and in the vascular groups of the Spätholz of the preceding year's wood, but also in all branches and leaves at a height of seven meters.

The translocation of sap in the lumen of the vessels was shown by STRASBURGER's experiments in which the cut surface of the exised branch was injected with a substance which liquified when cool. He injected the bases of shoots with fluid gelatin, cacao butter, or paraffin, and observed that the leaves wilted even though the cut surface was immersed in water. If a thin slice of wood were removed, thereby exposing the vessel walls, the amount of water translocated was not sufficient to prevent the wilting of leaves. The results of this experiment opposed successfully the imbibition theory of water movement in plants advanced by SACHS. STRASBURGER's work led to the conclusion that the ascent of sap in woody stems was not dependent upon living cells since it moved through sections killed by heat as well as by chemicals.

J. BÖHM had indeed attempted in 1863 to explain upon a physical basis the rise of fluids in stems but without great success. He also had shown that translocation could take place through a dead piece of stem but had been particularly unsuccessful in determining the nature of the forces involved. He made several inconsistent statements about the pressure differences in different cells and the rôle of atmospheric pressure in driving fluids from the tracheae into the leaf cells. BÖHM finally came to regard a simple capillary ascent as a sufficient explanation and his name is now remembered chiefly for his formulation of the capillary theory.

The understanding of the subject of sap ascent in stems was immensely advanced in 1894 when DIXON and JOLY published the first account of their theory in which the transpirational pull and the tensile strength of water columns were set forth. Briefly, DIXON maintained that the evaporation of water from leaves pulls the water in a continuous column through the tree. Although DIXON's theory was frowned upon by other physiologists of the late 19th century, it ultimately came to be regarded with favor. SACHS had discarded this theory on the grounds that there are no continuous tubes in plants, but DIXON and JOLY met the objection, stating that the water films may be regarded as continuous through the imbibed material of the transverse and oblique walls. DIXON assumed, in consonance with SACHS, that the moving water is located in the substance of the walls and that the surface tension forces developed at the surface of the fine-textured substance of the walls prevent the water column from becoming indefinitely attenuated. He concluded that the transpirational pull generated at the surface of the leaves is transmitted downwards through the imbibed water in the walls. Eventually DIXON and JOLY abandoned this modified Sachsian theory since it was ascertained that most of the water passed upward, not in the walls, but in the lumina of the vessels. The mechanism was demonstrated to depend on the tensile strength of a film of water in intimate contact with the walls of the tube which contains it.

ASKENASY experimentally demonstrated that the tensile strength of a moving water column was comparable to that in a tree in which the tension was caused by the evaporation of water from the leaves. Physicists have estimated the cohesive force of water to be 10 to 150 atmospheres, while DIXON estimated the cohesive force of the sap to be at least 100 atmospheres. The sap is possibly more stable under tension than pure water. To ascertain their power of drawing water from the conduits of the stem, DIXON measured the tensions generated in osmotically active leaf cells and reported that the leaf cells of *Acer macrophyllum* were capable of remaining turgescent and drawing up water against a pressure of 8 atmospheres. The osmotic attraction which would give rise to this pressure was calculated to be capable of raising a column of water to a height of 240 feet.

Initially DIXON and JOLY's conclusions met with objection because of the presence of gases in the sap. The opponents of the cohesion theory of water in vessels considered that the presence of air bubbles in the water would so weaken the columns that they would break. The objection was dispelled, however, when it was demonstrated that air bubbles do not usually enter a stem until it is severed. DIXON postulated that the tension in the sap in the tracheae is primarily responsible for the incursion of air when the stem is severed.

BODE studied (1923) the continuity of water columns in intact plants and obtained enlightening results. He removed some of the outer tissue from stems, leaving layers of living cells surrounding the conducting elements. His observations on *Impatiens, Tradescantia,* and other plants, made directly under the microscope, showed the water columns to be continuous even under conditions of such high transpiration or of such low water supply that the leaves were wilted. If the water columns were broken when under tensile stress the vapor phase expanded until it filled the

element and the column remained broken. If broken when water was at a pressure above zero atmospheres, the bubble slowly contracted and finally disappeared.

RENNER had concluded (1911) that the tension in the vessels contracts them, since when the top of a twig immersed in water is cut, the meniscus falls. BODE confirmed RENNER's conclusions by direct observation with the microscope, finding a consistent (except in three cases out of 32) increase in diameter after cutting the top. Stems killed by boiling in water for 15 minutes gave the same results as living stems, thereby refuting the argument of

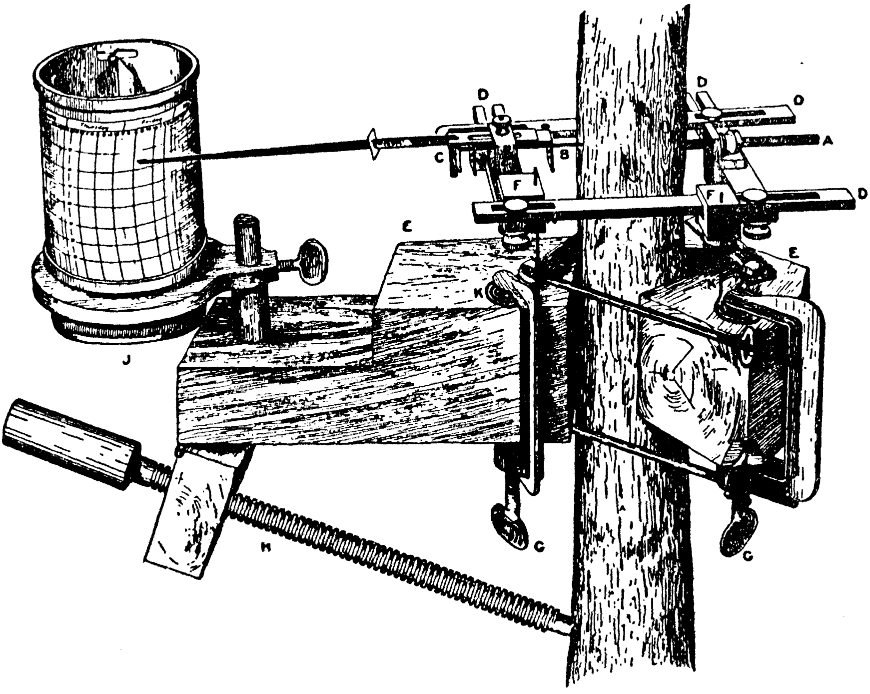


FIG. 24. — MACDOUGAL's dendrograph in position on a small tree trunk. The pen-lever traces a line on the paper chart on the revolving cylinder shown at the left. Reproduced by permission from Carnegie Institution of Washington, Publ. 462, p. 7 (1936).

the opponents of the cohesion theory who maintained that the contraction of living cells was responsible for the "Ruckstoss" phenomenon.

The validity of DIXON's conclusions concerning the state of tension in the vascular elements was established by MACDOUGAL's measurements of tree trunks by instruments which give a graphic record of shrinkage during or shortly after the periods of maximum transpirational activity, and the recovery following a period of minimum water loss. MACDOUGAL described (1929) the diurnal fluctuations in the diameter of the trunks of trees, both young and old, which give a striking demonstration of the concomitant stresses due to fluctuations in the transpiration pull on the water columns.

URSPRUNG and his associates undertook a critical study on the phenomenon of suction pressure as a factor in sap translocation

in plants. The existence of an equilibrium between osmotic pressure and the tension of the cell wall had been evident to DE VRIES and PFEFFER, each of whom formulated some useful ideas about the importance of turgor in maintaining the activities of the plant. URSPRUNG regarded osmotic pressure as the difference of pressure on solution and solvent which produces a condition of equilibrium such that there is no tendency of the solvent to flow in either direction. The absorbing function of cells is determined also by this equilibrium, not solely by the osmotic powers as earlier workers had assumed. URSPRUNG designated (1916 and later) the force which drives in water at any given stage of cell distention as the "suction force", or "suction pressure" of the cell, pointing out that the absorbing power of the cell, at any time, is equal to the osmotic value of the cell sap, minus the osmotic value of the external solution, minus the wall pressure. In order to measure the suction force of the cell, the concentration of the agent in which the volume of the cell is unchanged must be determined. URSPRUNG measured the suction force of the cell by determining the difference between the suction force of the cell sap and the wall pressure. Since the wall pressure in a plasmolyzed cell is zero, the suction force of the cell equals the suction force of its contents. In a cell at the point where it has reached saturation with water, the suction force of the cell content and the wall pressure are equal, hence the suction pressure is zero. There is a suction force gradient in the direction of the streaming water in the plant. The suction force of the root hairs may be used as an indicator for determining the relative resistance offered by soils to the influx of water into the plant. By measurements made in the field, URSPRUNG established (1926) the validity of his concept, finding that moisture of the soil and relative humidity of the air affected the suction force of the cells. The growth of cells thus paralleled the suction force; this is logical when one considers that increase in volume depends chiefly on the influx of water. The maximum growth of the cell does not coincide with the maximum turgor pressure, but with the minimum turgor or wall pressure and the maximum suction pressure.

The role of root pressure in sap flow was emphasized (1938) by WHITE who revived the interest in vital forces. The special technic which he devised utilized excised tomato roots growing in liquid media. The results indicated that root pressure was not overcome by opposing forces of 90 pounds per square inch. This pressure would be sufficient to raise water to a height of 200 feet. WHITE did not discount the importance of physical forces such as the transpirational pull, cohesion, and capillarity in the ascent of sap, but pointed out that root pressure may be a factor of greater importance than previously conceded.

Solute transport:- In addition to replacing the water lost by transpiration and so preventing desiccation, the movement of water in plants is intimately concerned in the transport of solutes both organic and inorganic.

The important phenomenon of translocation of solutes from one part of the plant to another was not intensively studied until the middle of the 19th century. When the earlier Aristotelian assumptions that the physiological processes in plants resembled

those of animals were forsaken there was nothing to take their place until recent years. In spite of a more or less tacit assumption that solutes ascend from the root upward in the xylem and descend in the phloem, a vast amount of work has been devoted to a reexamination of the subject. Due to a peculiar scientific myopia certain writers on the question of solute movements have failed to comprehend that it is intimately concerned with water movement. If substances are dissolved in the water, they move along, but first and last the stream is a water stream. We must not become so intent on the boats that we forget the river.

Although the ringing experiments of MALPIGHI, HALES, and KNIGHT showed an obvious relation between the bark tissue and the organic nutrition of the plant, real progress on the problem did not start until the work of HARTIG in 1837. His anatomical studies, coupled with ringing experiments and observations on phloem exudation, enabled him to develop an idea of a complete mechanism to explain the movement and storage of organic nutrients in plants. He regarded the sieve tube as a perforate element specially fit for the rapid conduction of solutes.

During the next 50 years there was an intensive study of phloem anatomy which clarified the phenomenon of organic nutrition. Although there was some disagreement concerning the question as to whether carbohydrates and organic nitrogenous compounds both move in sieve tubes, or whether the simpler carbohydrates passed through phloem parenchyma, the classical view of the sieve tube as a simple perforate element persisted and the mechanics of movement, though vaguely described, were not seriously questioned.

SACHS correctly apprehended the nature of the phenomenon of solute transfer and described the gradients which exist in a metabolising plant. He concluded that transport was due to diffusion from regions of higher to regions of lower concentration aided by the turgescence and tension of the tissues concerned, but clearly stated that there was a mass movement of substances through the sieve tubes and lacticiferous vessels, caused by the inequalities of pressure and by distortions and curvatures which the wind produces. SACHS therefore considered that, although the molecular diffusion of solutes might proceed without a corresponding water flow, there was a movement of water and solutes in the mass flow. His statements leave no doubt that he thought that sugars might pass the walls of parenchyma cells.

PFEFFER advanced (1876) some concepts which tended to support the foregoing assumptions on solute movement. He concluded, for example, that living protoplasts have the power of modifying their permeability to allow dissolved non-diosmosing substances to pass, and hinted that the plasmodesmata might afford a passage of solutes from cell to cell. He considered that streaming movements, which contributed to more rapid distribution of solute in the cell, might aid in translocation, but did not regard them as of general importance because he doubted whether streaming was a normal process in uninjured cells. The inorganic substances acquired by roots pass upward in the transpiration stream according to PFEFFER but he was less positive about the translocation of proteins, fats, and other metabolic products.

In the beginning of the 20th century, ideas generally accepted till then were questioned by new investigators who regarded many

of them as inadequate. RUHLAND declared (1912) that the sieve tube is no more permeable to sugars than phloem parenchyma; SCHMIDT regarded the sieve tube as a normal nucleate cell with no recognizable specialization for conduction; BIRCH-HIRSCHFELD abandoned (1919) the phloem as an adequate conductive tissue and attributed organic transport to a reversal of the normal movement of the transpiration stream; DIXON subscribed to the same view.

While the evidence for this belief was strong, convincing proof was not forthcoming. CURTIS criticised (1923) the prevalent views on the subject and made experiments which he interpreted to mean that the inorganic solutes may ascend the stem in the phloem. Most of his work, however, was concerned with the export of carbohydrates and other substances from the leaf, to the neglect of the movement of soil solutes. CURTIS laid emphasis (1935) on results of other workers which showed that water and salt absorption do not always proceed *pari passu,* although movement after absorption is influenced and determined by transpiration. His own experiments, however, did not demonstrate that soil solutes ascend the stem in the phloem.

MASON and his associates at the Cotton Research Station in Trinidad who studied the transport of solutes were unable to confirm CURTIS' conclusions. MASKELL and MASON reported (1929) that the major part of the mineral nitrogen absorbed by the roots ascended in the transpiration stream to the leaves of cotton plants whence, after being elaborated to amino-acids and other compounds, it was exported through the sieve tubes to the roots as organic nitrogen. Their conclusions were based upon data showing that the removal of a ring of bark from the stem did not appreciably affect the movement of inorganic nitrogen into the leaf, and that the total nitrogen of the leaf increased by day and diminished by night. Their work clearly showed that the migration of nitrogen and carbohydrate compounds in the stem is not wholly dependent on the flow of the water stream. The vertical gradients of total sugars and of organic crystalloid nitrogen in the bark were in opposite directions. The movement of carbohydrate was down a gradient of total sugars, while the movement of nitrogen was against a gradient of organic crystalloid nitrogen. They inferred that transport occurred in the sieve tubes by a diffusion process, accelerated in some unexplained way by energy released by respiration, and reported that the removal of a ring of bark from cotton plants was followed by a surplus amount of nitrogen in the stems and leaves above the ring, whereas CURTIS had reported the opposite effect.

CURTIS had reported that ringing a stem caused a reduction in transpiration, as a consequence of which the ringed branches would receive diminished quantities both of water and soil solutes. MASON, and his associate MASKELL, separated the whole foliar system of the plant from the root by the removal of a ring of bark and observed (a) an immediate accumulation of salts in the supraringed stem, (b) after a week a diminished translocation of solutes as the result of carbohydrate starvation of the roots, (c) a diminished quantity of salts in the ringed plants in comparison with intact plants. CLEMENTS attacked (1930) the problem in a slightly different manner. Starting experiments before new growth ap-

peared in the spring, he compared the nitrogen and ash content of stems before and after girdling. The nitrogen content of girdled branches had increased at the end of the season by as much as 220 times its original content, and, correspondingly, the ash content was 90 times the original. It thus appeared probable that the solutes which ascended through the region of the decorticated ring came from the soil and were carried in the transpiration stream.

Convincing evidence that the inorganic solutes rise in the xylem has been recently obtained (1939) by HOAGLAND and STOUT by the use of radio-active salts. They levered up strips of bark of *Salix* and inserted strips of waxed paper between bark and wood to prevent lateral movements. The bark was intact above and below the zone of separation. After the salts had ascended to the tips of the shoots, as shown by the Geiger counter, the lifted zone of bark was removed and tested. The amounts of the salts found in them were very small in comparison with the amounts in the wood and made it apparent that the ascent did not occur in the phloem elements.

CURTIS maintained that, while some of the solutes ascend in the wood, transport takes place also in the living cells of the phloem. When he chilled the petioles of bean leaves to a temperature slightly above freezing and enclosed them in an atmosphere of nitrogen the translocation of carbohydrate was stopped or at least greatly inhibited. From these and other experiments he concluded that translocation was dependent on living cells, and that protoplasmic streaming accelerated the diffusion in the sieve tube. Actual proof of protoplasmic streaming in sieve tubes is, however, hard to find and MASON and PHYLLIS rejected (1937) CURTIS' conclusion.

CRAFTS took up (1931) the histological aspects of the problem where VON MOHL and HARTIG had left them. He found that the pores in the sieve plate are not openings, but simply plasmodesmata surrounded by cylinders of callose and showed that the sieve tubes became permeable at maturity and demonstrated phloem exudation in a great variety of plants. Meanwhile MÜNCH demonstrated (1926) that the phenomenon of phloem exudation was a manifestation of the simultaneous transport of organic solutes and water through the phloem. The idea of an unidirectional mass flow of solutes in the sieve tube, originally proposed by HARTIG was reinvestigated by MÜNCH and CRAFTS. The theory of MÜNCH sought to give (1926) a complete explanation of the mechanism of solute movement in the phloem. It postulated that an area of high turgor pressure in the leaf and an area of low turgor pressure in the stem exist and that the pressure difference is sufficient to overcome the resistance in the intervening regions. His theory obviated the necessity for assuming that the sieve tubes take any active part in translocation, postulating that water moves along with the solutes and that under certain conditions the water must be liberated.

MÜNCH postulated a flow of solution under the impetus of a gradient of hydrostatic pressure ("pressure flow") in the sieve tubes through intervacuolar pores in the end walls. His theory controverted the evidence that transport is dependent upon the activities of living cells in the channels through which the solutes pass.

MASON, MASKELL, and PHYLLIS criticised (1936) the MÜNCH theory for the assumption of a uni-directional movement of all solutes under the total turgor gradient, whereas the proportions of different nutrients vary considerably from organ to organ and may also vary during the growth of organs.

SCHUMACHER made (1930) the first experimental demonstration proving that the sieve tube is the actual channel of transport of carbohydrate and nitrogen. He was able, by clever experimentation on *Pelargonium* leaves with a dilute solution of eosin, to close the pores in the sieve plates with callus, while the protoplasmic streaming in the phloem parenchyma was unchecked in the petioles. Since the flow of nitrogen and carbohydrate in such petioles was checked, he concluded that the transport of both these materials occurs in the sieve tubes. Although SCHUMACHER demonstrated movement of fluorescein in young phloem elements, the rates and conditions of movement are not such that the same mechanism could account for sugar movement. BENNETT and ESAU demonstrated (1936) that the movement of the curly top virus of sugar beet, after injection into the phloem by the beet leaf-hopper, shows that this virus moves with sugars along gradients that may be manipulated by altering conditions of sugar synthesis and utilization. This concurrent movement at similar rates of virus and sugars indicates a mass flow mechanism where diffusion plays only a secondary role as it determines pressure gradients.

CRAFTS emphasized (1931-36) the idea that there is a simultaneous movement of solute and solvent and maintained that any theory which involved a diffusion of the solute independently of the solvent was inadequate. He modified some of MÜNCH's ideas concerning the paths of the pressure-flow through the phloem by postulating that it moves through both the lumen and walls of the sieve tube; and concluded that the protoplasts of mature sieve tubes become permeable and allow a ready filtration of solution from element to element, as well as into and along the walls. From calculations of the resistance offered by the sieve plate and the wall he concluded that the resistance of the latter is small in comparison with the former, consequently the turgor pressure differences would be insufficient to force solutions through sieve plates whereas the resistance of walls was small enough to permit the passage of the entire pressure flow, or mass flow. The osmotic mechanism postulated by MÜNCH was operated by a turgor gradient between the source (*e.g.* the mesophyll) and the sink (*e.g.* non-green cells utilizing assimilates). CRAFTS maintained (1938) that an osmotic mechanism of that sort would not explain translocation from the seed piece of a potato into the turgid growing shoot and postulated that cells in the sink region, by accumulating assimilates against a gradient, maintain the pressure flow.

Further investigations will doubtless reveal the forces which are concerned in the movement not only of water, but also of the solutes through the phloem.

The foregoing paragraphs have given a fragmentary account of attempts to obtain reliable information about the conduits and the forces involved in solute migration. It should be apparent that the subject has received a vast amount of study since the time of SACHS. Although no definite agreement has been reached, it seems clear that the migration of solutes in the plant is dependent

upon some special organization of cytoplasm which for its maintenance and existence, requires an expenditure of metabolic energy.

Transpiration:- STEPHEN HALES was clearly aware of the effects of environmental factors on transpiration, as anyone may see by reading the account of his experiments published in "Vegetable Staticks" in 1727. In his writings, he spoke frequently of the accelerating effect of the "warmth of the sun", and of the diminished transpiration at night and on rainy days. But it was many a long year before anyone else undertook to study the problem scientifically. The determinations of environmental influences at first were largely qualitative, but eventually (in the opening years of the twentieth century) an increased interest in bioclimatic factors, leading to investigations on the important phenomena connected with transpiration, manifested itself.

A precise measurement of the external conditions which affect transpiration has been sought by physiologists and ecologists interested in relating plant activities to environmental conditions. The importance of the plant-water relations began to receive attention when ecology emerged from the descriptive and taxonomic phase at the beginning of the twentieth century. The relation of external conditions to transpiration received greater attention when ecological studies of plants were extended from cool, humid to hot, arid regions.

Atmospheric humidity. Since the evaporating power of the air is obviously related to the amount of moisture it contains, it is easy to understand that some of the first studies on environmental conditions were devoted to measuring the effects of the evaporating power of the air, since this determines to a large extent the rate of transpiration of plants. The ratio between T, the transpiration rate, and E, the evaporating power of the air, was termed "relative transpiration" by LIVINGSTON, who in that way attempted (1906) to measure the physiological behavior of the plant. To determine the evaporating power of the air, he exposed a porous-cup atmometer, consisting of a flask on which was mounted a porous porcelain candle. The apparatus was filled with distilled water and set up in the field. The loss of water was determined gravimetrically or volumetrically. In spite of certain limitations, the atmometer afforded an indication of the evaporating power of the air and has become a useful addition to experimental technique. LIVINGSTON has devoted much attention to the perfection of the atmometer and the technique of its use.

VAN TIEGHEM, observing that illumination accelerated transpiration, proposed (1886) the term "chlorovaporisation" to designate the evaporation of water by chloroplasts, since he believed that part of the radiations they absorbed would vaporize water. When it was understood later that the stomata opened in light and that the temperature of the entire leaf is elevated by illumination, the concept of chlorovaporisation was abandoned. FRANCIS DARWIN reported (1914) that there was a constant relationship between the relative humidity of the atmosphere and the transpiration rate of *Hedera helix* at a constant temperature. HENDERSON obtained results (1926) which, in general, agree with DARWIN's observation and he was able to amplify DARWIN's ideas of transpiration in an atmosphere of high humidity.

The water requirements of maize grown under different conditions of air humidity showed significant differences (MONTGOMERY and KIESSELBACH, 1912). Whether the water utilized was computed on the basis of dry weight produced or of leaf area, a greater amount was transpired in the drier condition. Although it is very desirable that the effect of the environment should be stated quantitatively if possible, no great success has yet been obtained. KIESSELBACH concluded (1916) on the basis of his findings, that no definite water requirement exists for a given species of plant, since, due to natural climatic differences, the requirements varied from year to year and in soils of varying fertility. The problem is complicated by the movement of the stomata which to a very marked degree regulates the amount of water passing through their orifices. The age of the leaf and the concentration of the cell sap have also been shown to modify the rate at which water is lost from the leaves. Experiments carried out by THUT (1938-39) confirm and extend the work of DARWIN on the relation between water loss and air humidity. THUT found that the water loss from leaves was an inverse linear function of the relative humidity. In a region of high relative humidity, however, water was absorbed by the leaves and not lost. The zero point of the water lost from the leaves to the humidity bottles was interpreted as the relative humidity of the stomatal openings and the intercellular spaces.

HESSELMAN studied (1904) the plants of the Swedish meadows and determined the effects of shaded and sunny localities on the transpiration rate, for which he employed the loss of weight of potted plants and the recession of water in potometers. He found that leaves with a strong development of palisade cells, when exposed to the sun, transpired far more than those with a weakly developed leaf structure.

A comprehensive study of the relation of evaporation and humidity to the distribution of vegetation in a marsh was made in 1909 by YAPP in Wicken Fen in Cambridgeshire, England. YAPP's work showed how extremely complex the problem really was, and paved the way for later work which broke up the problem into its component parts. By means of evaporimeters, he determined the evaporation at different levels in the field, finding immense variation in the average evaporation at three different levels. The air in the vegetation layer was very much more humid than that outside it. The higher and denser the vegetation, the greater the differences in atmospheric humidity between the upper and lower strata. The temperature measurements showed that the highest layers of vegetation possess a greater diurnal range of temperature than either the free air above, or the lower layers of vegetation. YAPP found that the transpiring organs which occupy the lower strata of the vegetation were not only in more humid air, but, in general, were under considerably more uniform conditions than those which reached "the general vegetation level".

Stomatal movement. The relation of stomata to transpiration was comprehended by many of the earlier physiologists, but their conceptions were often erroneous because of certain tendencies to over-simplification of the phenomenon. DE CANDOLLE stated (1832) that the escape of water vapor from plants was related to the number of stomata they contain and was clear in his statement

that light accelerates transpiration. The first painstaking investigation of the phenomenon of stomatal movement was made by VON MOHL (1856) in which he corrected the earlier misconceptions of the factors involved in opening and closing of guard cells. VON MOHL elucidated the whole subject by his discussion of the rôle of light and heat, as well as humidity, in determining the size of stomatal apertures. He showed that changes in shape of the stomata result from changes in the turgidity of the guard cells, but recognized that the movement is not independent of the turgor changes in other epidermal cells. SORAUER observed (1873) an inverse ratio between density of stomata on barley leaves and the water content of the soil in which they grew, however, the greater density on leaves in drier soil was chiefly due to the reduction in size of the epidermal cells of the leaves. It was not until 1878 that VON HÖHNEL demonstrated cuticular transpiration as well as stomatal transpiration, showing that the amount of transpiration depended upon the thickness of the cuticularized layer. The thick cuticle and the occurrence of wax were also studied by KOHL and others who followed VON HÖHNEL. LEITGEB considered (1886) that the turgor of the other epidermal cells is practically the only factor which determines the opening and closing of the guard cells. His mistakes arose from the observation that the guard cells close in the night and open in the day.

Enthusiasm for the importance of stomatal movements in regulating transpiration led some workers astray, and others to make certain teleological assumptions. SCHWENDENER attempted (1883) to arrive at a more nearly correct idea of the phenomenon, pointing out that stomata are concerned also with the entrance of CO_2 as well as the escape of water vapor from the leaf. FRANCIS DARWIN's work in 1898 on the phenomenon of stomatal movement gave a new appraisal of the factors concerned. Recognizing the importance of the turgor of the guard cells, he pointed out that changes in turgor are produced, not only by water, but also by alterations of a vital nature in the permeability of the protoplasm of the cells. He forecasted the direction of subsequent studies by suggesting that the turgor of guard cells may be regulated indirectly like other phenomena of irritability.

BROWN and ESCOMBE's discovery of the rapid diffusion of gases through small apertures gave (1900) a new view of the questions of transpiration and of assimilation. They arrived at some paradoxical conclusions and caused other workers to re-examine the problem. They showed, *e.g.*, that the open stomata of a sunflower leaf afforded passage for three to six times as much water vapor as anyone had ever observed previously. They found that the rates of diffusion through small apertures were proportional, not to the areas of the openings, but to the diameter. BROWN and ESCOMBE showed experimentally that no interference occurs in the rate of diffusion, provided the distance between the apertures is somewhat less than ten times their diameters. Under certain conditions the rate of diffusion may be practically as great as if no perforated membrane were present. This meant that the transpiration from the surface of a leaf bearing stomata was comparable to the amount of evaporation from a free water surface.

The increasing importance of quantitative measurements of stomatal openings impelled workers to invent new methods to re-

place the awkward methods initially employed. DARWIN and PERTZ devised (1911) a piece of apparatus, called a porometer, which could be attached to an intact leaf on the plant, without wounding it. The passage of air through stomata was indicated by the drop of a water column in the apparatus. The porometer gave more or less quantitative results and showed some conditions theretofore unappreciated by physiologists. LLOYD employed a method of direct measurement of stomatal apertures by which he stripped the epidermis and fixed it immediately in absolute alcohol. He ascertained (1909) that the regulation of stomatal apertures was not as simple as originally supposed since the stomata of some plants open in the morning but soon close again. MAXIMOV and others who have also worked with desert plants have confirmed and established the fact that the stomata of many plants under arid conditions remain open for a few hours in the morning, close before noon, and may remain closed the rest of the day and following night. MOLISCH devised (1912) a method of injecting stomata with liquids which permits direct observation of the stomatal conditions. He employed a liquid which is capable of wetting the cuticle of the leaf, *e.g.*, absolute alcohol, benzol, or xylol, and which penetrates and injects the intercellular spaces. The liquid will not penetrate, however, if the stomata are closed. He concluded that the stomata were widely open if alcohol penetrated, partially open if benzol enters but alcohol does not, nearly closed if xylol alone would inject the leaf, and completely closed if none of the liquids injected the leaf.

By means of these and other methods daily variations in stomatal conditions have been extensively investigated. LOFTFIELD extended (1921) the investigations on stomatal behavior in plants under arid conditions, demonstrating the effects of climatic and soil conditions and showing how various factors interact upon the leaf and its stomata.

The importance of internal factors on transpiration has recently been brought to light by the discoveries of KNIGHT. Noting that the transpiration rate was not always related to stomatal apertures, KNIGHT discovered (1916, 1917, 1922) that the water content of the mesophyll cells was an important factor. When the latter are turgid, the substomatal cavities are charged with water vapor, and transpiration will be rapid if the evaporating power of the outside air simultaneously removes the vapor from the surface of the leaf. He discovered also that the increase in transpiration which occurs in incipient wilting is accompanied by an increase in stomatal apertures, but that the subsequent decrease in transpiration is reached at a time when the stomatal apertures are still increasing, due to a decrease in the water content of the mesophyll cells. The cells of shade-plants lose their turgor when the water content has decreased very slightly; the cells of sun-plants, on the contrary, were found (1925) by Mme. KRASNOSELSKY-MAXIMOV to lose their turgor more slowly in the change from incipient to permanent wilting.

SCARTH demonstrated (1926 and 1927) that the H-ion concentration of the sap of the guard cells has an important influence upon stomatal movement. He found that the stomata of *Zebrina pendula* remained closed in an intermediate *p*H range (5.5-7.0), but opened in increasing concentrations of acid or alkali. Gener-

ally, the sap of guard cells was on the alkaline side when the stomata were open. He also observed that starch made its appearance in the H-ion range of closed stomata and disappeared when they were open, and that the changes were reversible.

Water balance. The earlier writers on physiology appear to have had no adequate conception of the water balance in plants and of its biological significance. Most of them devoted attention to a single aspect of the problem, neglecting to see that the water in a plant at a given moment is the difference between the intake and outgo under varying conditions. Gradually a concept of a daily water deficit was formulated, owing largely to the work performed in Arizona and in southern Russia. LIVINGSTON, ILJIN, MAXIMOV, and others have demonstrated important relations and have attempted to state them as precisely as possible, though it is often difficult to estimate the exact effect of the climatic and biological factors involved.

Observations made in various ways and on various plants subsequently established the existence of a diurnal water deficit. THODAY found (1909) that the area of the leaf during the middle of the day was appreciably reduced as a result of the losses of water to the air and that during the night it regained the loss due to shrinkage. The water deficits in the plant which occur under arid conditions were demonstrated (1912) by LIVINGSTON and BROWN and by Mme. KRASNOSELSKY-MAXIMOV (1917) each of whom made determinations of the actual water-content of plants. These workers showed that the deficits (depending upon the species) were large during the middle of the day, nevertheless, the deficits disappeared during the following night. Dendrographic records of the changes in volume of tree trunks and cacti obtained (1936) by MACDOUGAL showed that daily water deficits occur in massive plants whether in arid or humid habitats.

BRIGGS and SHANTZ made observations (1912) on pot cultures which showed that as the soil water was gradually exhausted, a time came when the rate of entrance of water into the lower part of the plant was surpassed by the rate of water lost. This is the condition of incipient drying. When the water content of the soil falls to a point where the plant roots are no longer able to obtain water from the soil particles, the plant becomes permanently wilted. BRIGGS and SHANTZ designated the water content of a soil at permanent wilting as the wilting coefficient of that particular soil. CALDWELL investigated (1913) the phenomenon of permanent wilting of plants and found that their water deficits were greatly in excess of those existing at the point of incipient wilting.

KOLKUNOV began investigations on drought resistance in 1905, attempting to trace a connection between the anatomical and physiological characters of cereals and emphasizing the relations between drought resistance and size of the cells. His conclusions were eventually severely criticized by other workers. The extensive results of work by BRIGGS and SHANTZ did not establish any evident relationships between the efficiency of transpiration and drought resistance though other important facts concerning water economy were discovered. Eventually they designated four classes of drought resisting plants, *viz.*: drought-escaping, drought-evading, drought-enduring, and drought-resisting. MAXIMOV considered (1916) that drought resistance of xerophytes would depend

upon their capacity to endure more prolonged and severe wilting than mesophytic plants. He emphasized the importance of this endurance phenomenon rather than the reduction of transpiration in xerophytism. He stated (1923) that xerophytic plants may lose half their water content without experiencing injury and that mesophytic plants, although losing comparatively little water, experience a reduction in dry weight constituents and ultimate abscission of the leaves.

Investigations of the physico-chemical properties of the sap of plants have endeavored to relate their osmotic pressure to drought resistance. DRABBLE and DRABBLE concluded (1907) that osmotic pressure varied directly with the physiological scarcity of water. FITTING, who studied (1911) the osmotic relations of plants of the Sahara, found that many plants devoid of water-storage tissues develop osmotic pressures in the cell sap ranging from 7 to 100 atm. WALTER investigated (1926-29) the maximum concentration of cell sap which plants can endure without permanent wilting. He determined in numerous xerophytes the osmotic concentrations of sap when the plants were in active growth, calling it the optimal osmotic concentration. He also determined the osmotic values in plants living under conditions of marked water deficit, calling these the maximal osmotic values. Upon the basis of these determinations WALTER proposed a critique of xerophytism. The differences between the optimal and maximal osmotic values in shade and mesophytic plants were small, but in plants of sunny, arid habitats (xerophytes) these differences were generally large. As a physiological approach to ecological and distributional problems WALTER's critique was very suggestive.

Noting the numerous examples in which there was no apparent relationship between cell sap concentration and drought resistance NEWTON and MARTIN examined (1930) the colloidal properties of expressed sap and concluded that they are important factors. Hydrophilic colloids bind water and increase the concentration of aqueous solutions. This "bound water" was stated to be a more reliable index of drought resistance than the osmotic pressure of the expressed sap. Osmotic pressure may be of more direct importance in absorption, but NEWTON and MARTIN estimated that imbibition pressure was more important in the retention of water by a plant under drought conditions.

The relations between the amounts of water transpired during the grand period of growth and the amounts of plant material produced claimed the attention first of agronomists and later of physiologists. SCHRÖDER corrected (1895) certain misapprehensions growing out of the work of the earlier investigations and showed that there was considerable difference in the water requirements of various cereals. He concluded that some correlation existed, not only between the water requirement and the intensity of transpiration, but also between water requirement and drought resistance. MONTGOMERY and KIESSELBACH (1912), KIESSELBACH (1916), BRIGGS and SHANTZ (1914, 1917) and SHANTZ and PIEMEISEL (1927) made extensive determinations of the water requirements of plants growing in the semi-arid regions of the United States in attempts to estimate the suitability of various agronomic plants for cultivation in a dry region. Although valuable information about the water economy of plants was obtained, the results were

not entirely conclusive, since other factors come into play in determining the relation of transpiration to dry weight of the plant.

MAXIMOV introduced (1917) the term "Efficiency of transpiration" to express the dry weight: transpired water ratio. He defined it as the amount of dry material accumulated per kg. of water transpired. The efficiency of transpiration of certain agronomic and steppe plants was studied at Tiflis by MAXIMOV and ALEXANDROV, giving them a basis for determining the degree of xerophytism. They found that plants which transpire most intensely use water less efficiently, *i.e.*, have a low efficiency of transpiration. Some of the plants showing a low efficiency are paradoxically semi-desert xerophytes. Annuals exhibiting conspicuous drought resistance, *e.g.*, corn and millet, had significantly high efficiency values. Other species exhibited intermediate values. MAXIMOV admitted that the values showed considerable variability and discussed at some length the effects of environmental factors upon the efficiency of transpiration.

Significance. There appears to be no unanimity of opinion concerning the biological significance of transpiration for the plant, notwithstanding the vast amount of study which separate aspects of transpiration have received. REINITZER raised (1881) the question whether transpiration is harmful, beneficial, or inconsequential for the plant. Having noted that plants of moist forests were more luxuriant than those of arid regions, he conducted experiments under bell jars through which he caused moist or dry air to flow. He concluded from his experiments and observations that transpiration is a necessary evil for the plant. VOLKENS considered (1887) it unlikely that transpiration is necessary for the existence of the world of higher plants, since submerged aquatics, no less than terrestrial plants growing in a continuously saturated atmosphere, can grow well. He arrived at no definite conclusion about the necessity of transpiration. HABERLANDT believed (1892) that the transpiration stream was an important vehicle for the movement of nutrient salts in the case of herbaceous plants, but that other forces should be invoked to explain the transport of nutrients in large woody plants since they ascend to the crown of large trees in the moist tropical forests.

PFEFFER summarized (1897) his view in a few conservatively phrased sentences:

> "Thus the rapid distribution of dissolved substances is in a large measure due to the transpiration current, and it is probable that trees and even herbs would be unable to obtain the required ash constituents in sufficient amount from the dilute solutions present in the soil by the slow process of diffusion. Transpiration probably aids gaseous exchange, and may also serve to prevent plants exposed to the sun from being overheated. It is moreover not impossible that transpiration and the processes connected with it exert influences upon growth and development which may be of the highest importance. How far this is true is doubtful as yet, but, on these grounds alone, it is possible that many plants may be quite unable to live and develop when transpiration is prevented". (EWART's translation Vol. 1, pp. 234-5).

CURTIS gave (1926) a critical discussion of the conclusions drawn by various writers on the subject, in which he pointed out their conflicting ideas. He found little evidence that transpiration was of undoubted benefit to the plant through its effect on the intake of water or solutes, since the absorption of nutrients is not

dependent upon water absorption. Since plants best adapted to hot regions are those which tend to reduce rather than favor transpiration, he decided that the alleged benefits from cooling have been greatly exaggerated. In general, he considered that transpiration rarely, if ever, has any appreciable beneficial influence. In opposition to the DIXON theory, CURTIS concluded that when the water supply is adequate and transpiration is not excessive, it probably has little influence on the life processes, on the contrary it may be detrimental if the amount of water in the soil is deficient or transpiration is excessive.

BOWER's contributions to the phylogeny of plants and their adaptive development have been mentioned in chapter X. It is sufficient for the moment to recall his ideas on the necessity for the development of surfaces exposed to the atmosphere and his statements on the importance of intercommunication between the members of the plant.

CLEMENTS summarized (1934) views on the utility of the transpiration process emphasizing the beneficial effects of transpiration through temperature stabilization of the plant; through the acceleration of the movement of inorganic solutes from root to leaf; through increasing the rate of photosynthesis; and through the stabilization of the internal nutrition of the plant.

Resumé:- The emergence of a science of plant physiology has been indicated in an earlier chapter in which the approach was made by HALES, INGENHOUSZ, SENEBIER, and others. The science of life phenomena had been singularly sterile for many centuries and the spirit of scholasticism tended to perpetuate the condition, for although that spirit was dying, it was not dead.

It was not so much the cynicism of the 18th as the spirit of honest inquiry in the 19th century that fostered the development of plant physiology. The haughty attitude of some self-crowned imperators of science which had formerly barred progress could not permanently check the spirit of research. Aided by the new discoveries in science and liberated from inhibitions against experimental work, men began to make significant discoveries about functions of plants. As a result of the work of the last century the problems of the water economy of the plant and the transport of solutes enjoy a position of scientific stability.

REFERENCES:-

BARTON-WRIGHT, E. C. (1933): Recent advances in plant physiology. Churchill, London.

BENNETT, C. W. (1937): Correlation between movement of the curly top virus and translocation of food in tobacco and sugar beet. Jour. Agr. Res. 54:479-502.

BRIGGS, L. J. and SHANTZ, H. L. (1912): The wilting coefficient and its indirect determination. Bot. Gaz. 53:20-37.

BURGERSTEIN, A. (1904): Die Transpiration der Pflanzen. Fischer, Jena.

CRAFTS, A. S. (1931): Movement of organic materials in plants. Plant Physiol. 6:1-41.

—— —— (1938): Translocation in plants. *Ibid.* 13:791-814.

CURTIS, O. F. (1926): What is the significance of transpiration? Science 63:267-271.

—— —— (1935): The translocation of solutes in plants. McGraw-Hill, New York.

DIXON, H. H. (1914): Transpiration and the ascent of sap in plants. Macmillan, London.

GREEN, J. R. (1909): A history of botany, 1860-1900. Clarendon Press, Oxford.

HARTIG, TH. (1858): Über die Bewegung des Saftes in den Holzpflanzen. Bot. Zeit. 16:329-335, 337-42.

HUBER, BRUNO (1924): Beiträge zur Kenntnis der Wasserbewegung in der Pflanze. Ber. Deutsch. Bot. Gesell. 42:27-32.

KNIGHT, T. A. (1801): Account of some experiments on the ascent of sap in trees. Phil. Trans. Roy. Soc. London 1801:333-353.

LIVINGSTON, B. E. (1906): The relation of desert plants to soil moisture and to evaporation. Carnegie Institution, Washington.

MACDOUGAL, D. T. (1929): Hydrostatic systems in trees. Carnegie Institution, Washington.

MASON, T. G. and MASKELL, E. J. (1928): Studies on the transport of carbohydrates in the cotton plant, I. A study of the diurnal variation in the carbohydrates of leaf, bark, and wood, and of the effects of ringing. Ann. Bot. 42:189-253.

—— —— (1928): II. The factors determining the rate and the direction of movement of sugars. *Ibid.* 42:571-636.

MAXIMOV, N. (1929): The plant in relation to water. Macmillan, New York. (transl. by R. H. YAPP).

MOHL, H. VON (1851): Grundzüge der Anatomie und Physiologie der vegetabilischen Zelle. Vieweg, Braunschweig. (transl. by HENFREY, 1852. London).

MÜNCH, E. (1926): Vortrag über Dynamik der Saftströmung. Ber. Deutsch. Bot. Gesell. 44:68-71.

SACHS, J. VON (1882): Textbook of botany. 2nd Ed., Clarendon Press, Oxford. (transl. by S. H. VINES).

STRASBURGER, E. (1891): Über den Bau und Verrichtungen der Leitungsbahnen in den Pflanzen. Fischer, Jena.

Chapter XIII.

THE FIXATION OF CARBON BY PLANTS.

The ability of plants to synthesize the greater part of their substance from gaseous constituents of the environment was still imperfectly understood at the beginning of the 19th century. DE SAUSSURE had, it is true, shown that atmospheric CO_2 is utilized by the green plant as a source of organic compounds, but after his work the doctrine of synthesis by plants was destined to have a long period of dormancy. This lack of appreciation of carbon assimilation prevailed with respect, not only to the work of DE SAUSSURE, but to that of PRIESTLEY, INGENHOUSZ, and SENEBIER. It was SACHS who first formulated (1882) a correct concept of the place of the living green plant in nature, and proclaimed that the formation of carbohydrates is the starting point for the production of all other organic compounds of the plant.

Since the time of ARISTOTLE there had been some notion, often vaguely expressed, of the effectiveness of the sun's rays to synthesize the substance of plants. DANTE wrote (Purgatorio XXV, vv. 77-78) "And that thou mayst marvel less at my words, look at the sun's heat, that is made wine when combined with the juice which flows from the vine" (CARLYLE-WICKSTEED transl., Modern Reader's Libr., New York, 1932).

The apparatus:- Although MALPIGHI, GREW and others had made some tentative statements about the omnipresent green pigment of plants, it remained for PELLETIER and CAVENTOU to give it the name "chlorophyll" in 1818. It goes without saying that those workers were unaware that the crude extracts which they prepared also contained pigments which are not green, but the name chlorophyll has been retained for the green pigment of plants which functions in photosynthetic assimilation of carbon.

The first chemists who studied chlorophyll made the unfortunate assumption that it is a comparatively stable chemical compound and, since they employed strong alkali or acid as a means of extraction, they were dealing with decomposition products of chlorophyll rather than with the substance itself.

STOKES advanced (1852) the knowledge of the optical properties of chlorophyll, later demonstrating (1864) that the chlorophyll of land plants is a mixture of four substances, two of which are green and two yellow, each possessing highly distinctive optical properties. He reported that the green substances yield solutions showing red fluorescence; the yellow substances do not. BERZELIUS postulated that biliverdin, the green substance obtained from bile, was identical with chlorophyll, but it was disproven by STOKES in 1864.

The erstwhile chaotic nature of the subject began to assume orderliness when FRÉMY demonstrated (1860) that by shaking an alcoholic extract of leaves with ether and HCl he could separate

a blue-green and a yellow pigment. It was not certain, however, whether the two fractions existed in the original extract or whether they were formed by the action of the acid; as a matter of fact nearly all the substances described by FRÉMY were products of decomposition, formed by the action either of acids or of alkalies on chlorophyll. Eventually it was found that one could extract a green and a yellow pigment from chlorophyll by the use of neutral solvents. KRAUS considered (1872) that the first was true chlorophyll and designated the second, which was distinctly different, as xanthophyll. Discussions of the chemistry of chlorophyll were rife for many years. Uncertainty prevailed whether the chlorophyll of all plants was identical.

DIPPEL found (1878) by the use of a spectroscope that KRAUS' green pigment contained a yellow pigment different from xanthophyll. BORODIN succeeded (1883) in isolating the crystals belonging to two groups of yellow pigments, one characterized by great solubility in alcohol and slight solubility in benzene, the other by a high solubility in benzene and slight solubility in alcohol. Other workers, using various methods, obtained discordant results. Carotin, one of the components of the yellow pigments isolated by FRÉMY and others, was discovered in the root of the carrot by WACKENRODER in 1827, and by BLEY in apricot fruits in 1835. STOKES' statement that there are two yellow pigments in leaves (1864) showed that he found a yellow lipoid though he said nothing about its relation to carotin. The researches of ARNAUD indicated (1885-7) that the crystalline yellow material which he found associated with chlorophyll was probably identical with carotin from carrot roots.

The confused state of knowledge prevailed, however, until the early years of the 20th century when TSWETT demonstrated (1906) that the different pigments in a leaf extract could be readily and distinctly separated by the use of inert agents. TSWETT filtered either a benzol, petroleum ether, or carbon disulfide extract (free from water) through finely divided solids in a glass tube. The pigments, owing to their differential adsorption by the adsorbent, were stratified in a very striking manner in the column and could be subsequently separated from one another by a knife. He thus separated two chlorophyll components which he called α-chlorophyllin and β-chlorophyllin, and five yellow pigments, designated carotinoids, and named, in ascending order of their adsorption; carotin (not adsorbed), xanthophyll α, xanthophyll α', xanthophyll α'' and xanthophyll β.

WILLSTÄTTER and associates finally put the chemistry of chlorophyll on a truly scientific basis and elucidated many difficult problems which had baffled their predecessors. His methods enabled him to obtain chlorophyll extracts unmixed with other substances which would have vitiated the results. WILLSTÄTTER'S first paper was published jointly with MIEG in 1906 and was entitled "Über eine Methode der Trennung und Bestimmung von Chlorophyllderivaten." By his successful methods of extraction he was able to get material suitable for exact chemical study from various species of various families of plants, and from plants growing under different environmental conditions.

Limitations imposed by the nature of this volume forbid an extended discussion of the complicated chemistry of chlorophyll

and its derivatives. Briefly stated, WILLSTÄTTER's researches showed that the chloroplasts contain four pigments, two green and two yellow.

These are:

1. Chlorophyll *a*, $C_{55}H_{72}O_5N_4Mg + \frac{1}{2} H_2O$, blue black in the solid state, blue green in solution.
2. Chlorophyll *b*, $C_{55}H_{70}O_6N_4Mg$, green black in the solid state, pure green in solution.
3. Carotin, $C_{40}H_{56}$, forming orange yellow crystals.
4. Xanthophyll, $C_{40}H_{56}O_2$, forming yellow crystals.

These are substantially the same as those described by TSWETT, except that WILLSTÄTTER could not distinguish the four forms of xanthophyll. In fresh leaves the four pigments were found in approximately the following quantities, expressed as parts per thousand: chlorophyll *a*, 2; chlorophyll *b*, 3/4; carotin, 1/6; xanthophyll 1/3. Although it is known that chlorophyll is the pigment directly involved in photosynthesis, the role of the various components and of the carotenoids is, as yet, unexplained. TSWETT proposed (1906) that the yellow pigments should be designated carotenoids. Owing to difficulties in separating them in their pure state, many investigators were skeptical about the existence of several yellow pigments. All doubt upon the subject was removed when WILLSTÄTTER and MIEG isolated (1907) and crystallized carotin and xanthophyll. They found that these substances may be quantitatively separated by their differential solubility in petroleum ether and 90% methyl alcohol. Carotin is soluble in the first, and xanthophyll in the second solvent.

A number of the earlier writers ventured the opinion that chlorophyll might be formed directly from one or the other of these yellow pigments but the idea has not been confirmed. Carotin is a hydrocarbon, whereas chlorophyll *a* and *b* are complex substances containing pyrrol rings. Relations between the amounts of chlorophyll and of carotin have been reported (1929) by EULER, by SJOBERG in 1931, and by MACKINNEY in 1935. The ratio of chlorophyll to carotin was more constant than to xanthophyll. Chlorophyll and carotenoids in barley seedlings, in general, fluctuated together, though the carotin/xanthophyll ratio was lower in chlorotic leaves.

The brown algae were studied in 1865 by COHN who believed that they contain a brown pigment called phaeophyll presumably related to chlorophyll. TSWETT later alleged (1905, 1911) that the brown algae contain chlorophyll like other plants but that it is masked by yellow pigments. The change in color from brown to green when a thallus is immersed in boiling water was supposed to be due to the release of the brown masking pigment, or to the alteration of the yellow pigment. TSWETT also alleged that the brown algae contained a third chlorophyll which he designated chlorophyll γ. WILLSTÄTTER and PAGE clarified the problem when they showed that the brown algae contain, in addition to the pigments common to green plants, another carotenoid with the composition $C_{40}H_{56}O_6$ to which the name fucoxanthin has been given. Many other carotenoid pigments have been isolated from plants in recent years and the number will undoubtedly increase.

The relation of wave length of light to carbon fixation has been frequently investigated since DAUBENY made his experiments in

1836. SACHS' experiments with solutions of potassium bichromate and ammoniacal copper oxide in double walled bell-jars demonstrated (1864) that the decomposition of CO_2 proceeded almost as energetically in the reddish-yellow as in full sunlight, and that very little decomposition occurred in the blue. TIMIRIAZEFF studied (1875) the decomposition of CO_2 in leaves placed in different parts of the spectrum; and ENGELMANN devised (1881) the well-known bacterial method which shows the liberation of O_2 from alga filaments. There was general agreement that the greatest activity occurs in the region of the B and C lines in the spectrum, however, when other pigments than chlorophyll are present (as in the red or brown algae) the maximum fixation of carbon may fall in another part of the spectrum.

BREWSTER's observations made in 1834 on the spectrum of chlorophyll remained isolated until about 1872 when TIMIRIAZEFF, PFEFFER, MÜLLER, and LOMMEL independently undertook some investigations on the relation between the absorption spectrum and the efficiency of photosynthesis. No little confusion prevailed among the conclusions of the above mentioned investigators and SACHS was contemptuous of the entire subject. Their results seemed either to explain too much or too little. They started from HERSCHEL's assumption that a photo-chemical reaction may be produced only by those rays that are absorbed by the substance undergoing a change. One of the difficulties in applying HERSCHEL's law was pointed out by TIMIRIAZEFF, *viz.*, that light was absorbed by chlorophyll and not by carbon dioxide, yet it is the latter which undergoes chemical change. He suggested, therefore, that chlorophyll acts as a sensitizer which absorbs the rays and enables them to institute chemical changes in the carbon dioxide. LOMMEL advanced (1871) the idea that the rays in the part of the spectrum between the B and C lines in the red which are most completely absorbed by chlorophyll are the most efficient in photosynthesis. The results obtained by TIMIRIAZEFF and by REINKE supported this idea. ENGELMANN, who employed a method utilizing motile bacteria as indicators of oxygen liberation from an algal filament, found (1882, 1884) a secondary maximum of photosynthetic activity in the blue violet part of the spectrum as well as in the primary maximum in the red.

PFEFFER, ignoring the fluorescence of chloroplasts, pointed out that it is of the utmost importance that light which has already passed through a chloroplast should still be able to be used in assimilation, for it is impossible in an ordinary leaf for all the chloroplasts to be exposed to direct illumination. PFEFFER and others believed that the photosynthetic activity of the leaf depended to a great extent upon the intensity of the illumination. The difficulties of interpretation are indicated by the results of SEYBOLD published in 1932 and 1933 showing the differences in the spectra of a green leaf and the chlorophyll extracted from it.

The phenomenon of fluorescence which has been frequently investigated is most readily and plainly seen in chlorophyll solutions. The fluorescence of chlorophyll and the absorption spectrum of a chlorophyll solution were discovered in 1834 by BREWSTER, although the descriptions by NEHEMIAH GREW imply that he saw fluorescence in extracts of leaves which he obtained by means of oil. **Physiologists have assumed rather tacitly that there is significance**

attached to the fact that chlorophylls are fluorescent substances, especially in regard to the transference of energy. TSWETT indicated (1901, 1911) that in light chlorophyll undergoes a change, resulting in the formation of an isomer of higher energy content. Subsequently the isomer changes back to the original form with evolution of the absorbed energy as phosphorescent light which is absorbed by the carbon dioxide.

ZSCHEILE concluded (1935) that the fluorescent properties of chlorophyll are intimately associated with the absorption of radiant energy and its conversion into chemical energy as one part of photosynthesis. While it is thought by recent investigators that the property of fluorescence is intimately connected with photosynthesis, there are many who regard the evidence as unconvincing, since living chloroplasts show fluorescence so faintly and colloidal solutions of chlorophyll show none.

The eminent chemist, HOPPE-SEYLER, started a series of investigations upon chlorophyll in 1879 which, he believed, supported the idea of a relationship between chlorophyll and hemin. He employed boiling alcohol for a solvent, wisely avoiding the use of acids or alkalies, the materials he thus extracted from fresh grass were separated and purified, yielding a crystallizable substance which he designated chlorophyllan. His misfortune lay in the fact that it was not chlorophyll. The pigments had been changed by the action of liberated plant acids and by the boiling alcohol and contained an appreciable amount of phosphorus. HOPPE-SEYLER concluded that chlorophyll belonged to the lecithins. In spite of these errors HOPPE-SEYLER did some valuable work on the chemistry of chlorophyll and stimulated others to undertake studies of the problem.

VERDEIL suggested (1858) that there is a similarity between chlorophyll and blood pigments. Originally it was supposed that the chlorophyll molecule contained iron.

In the latter part of the 19th and early part of the 20th centuries there were other attempts to establish a homology between chlorophyll, the green pigment of plants, and hemin, the red pigment of blood. MARCHLEWSKI was greatly interested (1909) in this similarity, but WILLSTÄTTER and others have failed to establish any constitutional relationship between the two. When the pure chlorophyll was analyzed it was found to contain, not iron, but magnesium. Hemin contains iron. In chlorophyll there is ester formation with phytol, in hemin a combination with globulin. These suggestions of chemical relationships between hemin and chlorophyll were based largely upon the similarity in constitution of compounds derived from the two substances. Chlorophyll and hemin were traced back to the same etioporphyrin, $C_{31}H_{36}N_4$, which may be regarded as a parent substance, and it is probably to it that chlorophyll owes its characteristic properties. The best dissertation on the relation of chlorophyll to hemin is undoubtedly that of MARCHLEWSKI, published in 1909, in which the absorption spectra of the two were assiduously studied and measured.

Plastids:- The structure of the plastid which was first thoroughly investigated by PRINGSHEIM in 1874 has been the subject of many investigations and of controversial discussions. PRINGSHEIM concluded that the oily pigment is held in the stroma of

the plastid, which has a sponge structure. TIMIRIAZEFF held (1903) that the pigment forms a layer on the surface of the stroma which is otherwise colorless. TSWETT assumed (1901) that the pigment is adsorbed on the surface of the stroma of the plastid, PALLADIN suggested (1910) that chlorophyll in the plastids is combined with lipoid materials, possibly in some form of chemical combination. PRIESTLEY and IRVING also considered (1907) that chlorophyll is restricted to the peripheral ring of the chloroplast, where it is held in the meshes of a network of protoplasm in the two species of *Selaginella* they studied.

The actual state in which chlorophyll exists in the plastid is a difficult matter to determine. WILLSTÄTTER concluded that it must be in a colloidal mixture because pure solvents such as acetone, ether, and benzene do not extract the chlorophyll from dried leaves, but do so at once if a little water is added. He explained (1913) the phenomenon by saying that the added water dissolved salts present in the dried leaves, and that the salt solution thus formed changes the colloidal state of the chlorophyll in the plastid and makes it easily soluble. Based upon evidence obtained from the spectrum and from fluorescence, STERN came to the conclusion (1920) that the chlorophyll must be in true solution in the plastid, dissolved probably in lecithin or some allied lipoid compound. According to him the chloroplast is an emulsion or emulsoid with a chlorophyll-lipoid phase and an aqueous-protein phase.

The chlorophyll unit:- To more than one writer the confused, and often contradictory, assumptions concerning the assemblage of chlorophyll molecules necessary for photosynthesis have appeared particularly futile. The first assumption usually required supplementary assumptions in which imaginary compounds were peculiarly abundant. It was impossible to study this synthesizing action of chlorophyll outside of the living cell; hence the failure of the conventional methods of the chemist.

It has been variously estimated that from 1000 to 3000 molecules of chlorophyll are required to form an actively functioning unit in photosynthesis. There was more or less agreement that the number of chlorophyll molecules greatly exceeded the number of instantaneously reducible carbon dioxide molecules, and that the number might vary from species to species, or indeed, from time to time in a given species.

EMERSON concluded (1936) that the so-called chlorophyll unit may represent the ratio between chlorophyll and some other internal factor, perhaps the substance which combines with carbon dioxide.

Production of chlorophyll:- The origin of chlorophyll early attracted the attention of investigators. GRIS showed (1844) that iron is necessary for the formation of chlorophyll and others thought that it was a constituent part of the molecule until more exact methods of analysis disproved the idea. It is now known that iron is necessary for the formation of pyrrol rings in the chlorophyll molecule. Several other mineral elements are necessary for the production of green color in plants. Magnesium, one of the constituents of chlorophyll, was shown (REED, 1907) to be

indispensable. REED and DUFRÉNOY described (1935) the role of zinc in the production and maintenance of chlorophyll.

PALLADIN reported (1891) that sugars are essential for the production of chlorophyll in the plant. He showed that etiolated leaves of wheat, barley, and other plants contained much soluble carbohydrate material, while those of bean and lupine contained little. If etiolated leaves of the former were floated on water in the light, they became green, while those of the latter did not regain their green color except when floated upon a sugar solution.

CORRENS demonstrated (1892) that the presence of oxygen was an additional factor necessary for chlorophyll formation, although the leaves were illuminated. A small amount of oxygen was insufficient, an excess was necessary for greening the leaves.

SACHS in 1864 and WIESNER in 1877 showed the influence of temperature on the development of chlorophyll in plants. The latter found that the optimum temperature for its production in etiolated barley seedlings was between 18° and 30°C. ELFVING discovered (1880) that in minimum temperatures illumination of etiolated leaves produced a deeper yellow color in the plastids, and concluded that light increased the amount of etiolin instead of chlorophyll.

The oft-repeated observation that plants deprived of light lose their green color was discussed in 1859 by SACHS who showed that in light of moderate intensity decomposition and recomposition of the pigment goes on continuously. SAYRE investigated (1928) the effect of light of different wave lengths on the formation of chlorophyll in seedlings of various plants. For equal energy values, the red were more effective than the green rays, and the green more than the blue. Radiations possessing wave lengths greater than $680\mu\mu$ were not effective in the formation of chlorophyll, but all other regions of the visible spectrum to $300\mu\mu$ were effective, providing the energy content was sufficient.

TIMIRIAZEFF attempted (1903) to determine whether the system protochlorophyll $\rightleftarrows$ chlorophyll is an oxidation-reduction system. Reduction of chlorophyll in pyridine with zinc and an organic acid yielded a colorless solution which did not show the characteristic chlorophyll spectrum. In contact with the air the green color and the specific optical properties of chlorophyll gradually returned. TIMIRIAZEFF gave the name protophyllin to this colorless reduced compound. ROTHEMUND considered (1935) that this reaction cannot be explained as a reversible hydrogenation and dehydrogenation of the chlorophylls since the reoxidized solutions are different from the chlorophylls subjected to the reaction.

When the subject of chlorophyll production began to be investigated it was discovered that there were certain precursors which played an important role in the development of the pigment. Among these was the substance designated leucophyll. LIRO claimed (1908) that the rate of change of leucophyll into chlorophyll is proportional to the light intensity, as long as enough leucophyll remains to be transformed, after which the rate of chlorophyll production slows down as it is limited by the rate of production of new quantities of leucophyll. LIRO concluded that protochlorophyll cannot be converted into chlorophyll. He thought that the production of chlorophyll from leucophyll is not dependent on the activity of the living cell, as it may proceed even in dry

leaf tissue, but it is dependent upon temperature. LIRO claimed that if the plant tissues die slowly in the hydrated condition, the leucophyll is changed into the green pigment, protochlorophyll. The same change also occurs if the tissues are extracted in alcohol. When these etiolated seedlings are carefully dried, the leucophyll is preserved and is able to yield chlorophyll if exposed to light.

The substance designated etiolin by earlier writers was designated protochlorophyll by MONTEVERDE who extracted it from wheat, maize, and sunflower by means of 95% alcohol. GREILACH who obtained protochlorophyll from barley and other seedlings believed that, under the influence of light, protochlorophyll was transformed into chlorophyll, but protochlorophyll has never been prepared in the pure state, neither has it been transformed into chlorophyll *in vitro*. By treatment of protochlorophyll with acids or alkalies, LUBIMENKO and MONTEVERDE obtained (1909) derivatives similar to those obtained from chlorophyll. LUBIMENKO in a later paper assumed that the pigment of chloro- or chromoplasts is derived from a fundamental precursor substance, which he termed "leucophyll", which is the precursor of protochlorophyll and all other related substances. He unfortunately introduced a number of terms into his discussion, which made it difficult to compare his ideas with those of other investigators. LUBIMENKO and MONTEVERDE designated the substance in etiolated plants which immediately changes into chlorophyll in the presence of light as "chlorophyllogen". When all the chlorophyllogen in an etiolated plant was converted into chlorophyll, the action of enzymes reconverted chlorophyll into chlorophyllogen. The formation of chlorophyll was inhibited by light of too great intensity.

LUBIMENKO described (1927 and 1928) the pigments of the plastids and traced their transformations from one substance into another. He summarized (1932) his ideas of the successive reactions in chlorophyll formation in the following steps.

1. Synthesis of leucophyll (a colorless substance).
2. Transformation of leucophyll into chlorophyllogen (a green substance).
3. Transformation of chlorophyllogen into chlorophyll.

Reactions 1 and 2 occur in the dark, reaction 3 is strictly photochemical.

Mechanism of photosynthesis:- The essential steps in the process of the formation of carbohydrates by the photosynthetic activities of the leaf were not comprehended in even an elementary fashion until the middle of the 19th century. PRIESTLEY, INGENHOUSZ and others had been concerned with the effects that plants had on the air, DE SAUSSURE and SENEBIER had comprehended some of the functions of the plant in assimilating carbon dioxide, and the former was explicit in his statements that water was fixed along with CO_2. DUTROCHET had discovered that the absorption of CO_2 and the release of oxygen occurred only in cells containing the green substance which PELLETIER and CAVENTOU had described.

It was SACHS who initiated the scientific study of the synthetic powers of the green leaf. He produced (1862 and 1864) the first scientific evidence that the starch present in the green cells (pre-

viously observed by VON MOHL and NÄGELI) is a product of the CO_2 absorbed, and formulated the statement, which subsequently became almost axiomatic, that starch is the first visible product of photosynthesis. His opinion was based upon observations on the distribution of starch in plants and also upon the disappearance of starch if leaves were kept for several days in darkness. Subsequently starch was again formed if the leaves were exposed to light. BOUSSINGAULT at that time (1864) demonstrated that the volume of O_2 evolved in the process is approximately equal to the volume of CO_2 absorbed, thus supporting a suggestion made earlier by DE SAUSSURE.

The concept that the pigment enables the cell to assimilate carbon dioxide only when associated with a plastid was formulated (1864) by BOUSSINGAULT; and PFEFFER showed (1881) that plastids without chlorophyll are unable, though illuminated, to produce carbohydrates. In other words photosynthesis is a process confined to living cells. PFEFFER (1896) and EWART (1896) showed that various physical and chemical factors may inactivate the chloroplasts (*e.g.* heat, irrespirable gases, narcosis, dilute acids and alkalies, strongly plasmolysing solutions, etc.). The results led them to conclude that, the stroma of the chloroplast being paralyzed, the chlorophyll pigment, alone, was unable to carry on the process of photosynthesis. KNY found (1897) that photo-assimilation was not accomplished by chlorophyll after having been extracted from dried leaves, a result confirmed by many others.

The effect of the concentration of carbohydrate in the leaf upon the rate of photosynthesis was clearly demonstrated by SAPOSCHNIKOFF in 1890 and 1893 in detached leaves of *Vitis labrusca* and *Vitis vinifera*. Photosynthesis ceased when the carbohydrate content of the former reached 17 to 25 percent of the dry weight and 23 to 29 percent in the latter. This inhibition of the process has been confirmed by others with other plants.

The consensus of opinion of recent writers is that carbon dioxide must combine with chlorophyll in order to be reduced and this occurs in a number of steps, requiring the successive absorption of four quanta of visible light. As a result of the rearrangements required to obtain formaldehyde from carbon dioxide, some sort of peroxide is formed. Its subsequent decomposition with the liberation of oxygen by the enzyme catalase is supposed to constitute the "Blackman reaction".

Within recent times there have been serious attempts to elucidate the mechanism of the process. WILLSTÄTTER and STOLL postulated (1918) that there are at least six reactions involved in the production of a sugar from carbon dioxide and water. These are: (1) the diffusion stage; (2) the absorption of CO_2 by plant amino acids or proteins; (3) the formation of an addition compound between chlorophyll and CO_2; (4) the photochemical isomerization of the addition compound; (5) the separation of oxygen and formaldehyde from the isomer by an enzyme with a re-formation of the original chlorophyll; and finally (6) the polymerization of formaldehyde into sugar.

NOACK assumed (1920) that the photosynthetic process consists of three steps: (1) a change of the fluorescent chlorophyll under the action of light and by absorption of oxygen into a peroxide; (2) a conversion of CO_2 into a peroxide form without the aid of

light energy; and (3) a mutual reduction of the two peroxides with evolution of oxygen, the re-formation of chlorophyll and the production of the grouping $HO\text{—}\overset{|}{\underset{|}{C}}\text{—}H$ which would easily condense to carbohydrates. FRANCK also concluded (1935) that chlorophyll must be partially photo-oxidized before the energy it absorbs can be used for CO_2 reduction.

The theory of WARBURG postulated (1919 *et seq.*) that there were three essential steps in the phenomenon of photosynthesis; *viz.*, (1) the photochemical primary reaction; (2) the secondary reaction; and (3) the acceptor formation. Light, acting on the chlorophyll molecule, would form the photochemical primary product at a rate proportional to the amount of radiant energy absorbed per unit time. The second step consists of a reaction between this product and the "acceptor" in which no substances are formed which automatically release oxygen. The third step (the "dark reaction") takes place independently of light in which, according to WARBURG, the "acceptor" is formed. This reaction he designated as the "Blackman reaction". The term "Blackman reaction" as used in reference to photosynthesis was coined by WARBURG who applied it to an ordinary chemical reaction which is associated with the protoplasmic activity of the cell. It is affected by temperature changes and is sensitive to narcotics. WILLSTÄTTER and STOLL considered (1918) that the "Blackman reaction" consists in the cleavage of oxygen from a peroxide which is formed in the reduction of carbonic acid. Subsequently WARBURG relinquished his theory and adopted that of WILLSTÄTTER and STOLL.

WILLSTÄTTER and STOLL offered (1932 and 1933) strong evidence that chlorophyll acts not only as a sensitizer, but that it enters into the course of the chemical reactions. Chlorophyll having two especially loosely bound hydrogen atoms is assumed to give off these atoms in reducing CO_2 and to regain the hydrogen by dissociating water. They believe that the presence of oxygen is necessary to start photosynthesis. Therefore they assumed that monodehydrochlorophyll and not the fully dehydrogenated chlorophyll is the substance which enters into the reactions of photosynthesis.

VAN NIEL regarded (1935) photosynthesis as a process of hydrogenation of CO_2, rather than a reduction of carbonic acid. Since four light quanta are apparently the minimum number which must be absorbed in order to reduce one molecule of CO_2 to formaldehyde, he concluded that the primary action of light may be to produce active hydrogen. He laid emphasis on this point since he had observed that purple bacteria reduce CO_2 but produce no oxygen, despite the fact that they are abundantly supplied with catalase. He pointed out that purple bacteria require special hydrogen donors such as oxidizable sulfur compounds, fatty acids, or even gaseous hydrogen, while the green plants use water as a hydrogen donor. Although it is difficult to assume that the absorption of light by green cells produces active hydrogen atoms, there appear to be some advantages in VAN NIEL's hypothesis. In the main it is simpler than some of those formerly proposed, *e.g.* each absorbed quantum is supposed to do the same thing, namely, produce one atom of hydrogen.

Energy relations:- The kinetic relations of photosynthesis were first appreciated and formulated in 1847 when JULIUS ROB. MAYER, the discoverer of the Law of the Conservation of Energy, announced that plants acquire solar energy and store it in a fixed form. Since his time there has been a growing appreciation that all the higher forms of life on the earth depend on the energy that comes from the sun through the agency of the green plant.

A host of investigators have undertaken quantitative studies on the degree to which green plants store the solar energy and the amount which passes out unused. In the beginning the calculations were approximations, but refinements of technique were found later. PFEFFER assumed (1871) that a square meter of the leaf surface of *Nerium* formed starch at the rate of 0.000535 g. per sec. Estimating the heat of combustion of starch as 4100 calories per g. he concluded that 2.2 calories of solar energy was used per sq. m. per sec., which would be less than 1 percent of the total solar energy available. This unexpectedly low percentage was confirmed by measurements of TIMIRIAZEFF. DETLEFSEN made (1888) observations on the absorption of light in a leaf by means of a thermopile, placing the leaf alternately in air containing 10 percent CO_2 and in air free from that gas. In the former case in which assimilation proceeded, he found that more light was absorbed than when there was no assimilation. Although his results were vitiated by various experimental errors, he confirmed earlier conclusions that the percentage of CO_2 fixed is small.

BROWN and ESCOMBE made an extensive study (1905) of the kinetic relations of the green leaf. Instead of using the amounts of starch formed, or of CO_2 assimilated, they measured the amount of radiant energy absorbed and transformed into heat with a pair of differential platinum thermometers. Theirs was by all odds the most important work on this problem up to that time, and marked the road for future studies. They determined as well as possible (1) the total amount of solar radiant energy which impinged on a leaf in a given time, (2) the amount which was absorbed (coefficient of absorption), (3) the measure of internal work of the leaf due to (a) water vaporization, and (b) photosynthesis, and (4) the influence of air movement on the thermal emissivity of the leaf. The energy used for transpiration was many times greater than that used for photosynthesis. The percent of energy used in photosynthesis naturally varied with the intensity of the light. For example, as little as 0.5 percent of the total incident radiation received in full sunshine was used in photosynthesis whereas as much as 4.5 percent was used when the light was reduced to only 13 percent of its former intensity. They emphasized that the leaf possesses a power of selective absorption due mainly to its specific coloring matter. BROWN and ESCOMBE's work which has been extended subsequently by others came down to this: the green plant uses only a very small part of the solar energy in photosynthesis since it is, under conditions of ordinary illumination, limited by some other factor.

LUBIMENKO observed (1905 and 1908) that shade plants could accomplish a given amount of photosynthesis with weaker illumination than sun plants and that the chlorophyll content of the former was greater than that of the latter.

FRANCK summarized recent conclusions on the energy relations of photosynthesis in the following statements. Four light quanta which are absorbed by chlorophyll and transferred to the carbon dioxide are used to reduce one CO_2 molecule to formaldehyde and to set free one oxygen molecule. The result is in good agreement with thermochemical relations. The energy required to reduce CO_2 and water to formaldehyde and H_2O_2 is equal to the energy of 3½ light quanta of red light. As an intermediate stage between CO_2 and formaldehyde the formation of formic acid is assumed.

The former value of the quanta required has been valued variously by others since WARBURG made the original estimation. EMERSON has recently placed its value at approximately 10.

The induction period in photosynthesis was described (1918) by OSTERHOUT and HAAS as a result of the observation that about two hours were necessary for the attainment of a steady rate in the marine alga *Ulva*. By means of other methods other investigators have observed shorter induction periods, not only in algae, but in flowering plants. BRIGGS surmised (1933) that the long induction period in *Ulva* observed by OSTERHOUT and HAAS after long periods in darkness might be due to a shortage of oxygen in the cells. In other words that anaerobiosis might have some connection with the production of an inhibitor.

OSTERHOUT and BRIGGS each have formulated ideas of a chain reaction, which in its simplest form (BRIGGS, 1933) is represented by the formula

$$S = S_i + S_i + S_f$$

meaning that there may exist in assimilating cells a substance S, which can be activated by light energy to a form S_i which then breaks down to reform unactivated free substance S_f and the products of assimilation. When the S substance combines with an inhibitor *i*, the substance S_i is formed. From this representation BRIGGS proceeded to discuss the theoretical aspects of the induction period in relation to the rate of oxidation and the production of oxygen in the photosynthetic process.

According to FRANCK and HERZFELD (1937) it is possible that much of the chlorophyll may be attached to intermediate respiratory products, such as plant acids, after a long dark period. Illumination could then cause photosynthesis, as in the case of chlorophyll-carbonic acid or chlorophyll-formic acid complexes. They assumed that it was probable that photo-oxidation of these plant acids, probably by a chain mechanism, might also occur. Until the accumulated respiratory products were exhausted, this oxygen consumption would largely counterbalance the photosynthetic oxygen production, thus causing an induction period.

EMERSON criticised (1937) not only the kinetic theory of BRIGGS, but others, averring that where nearly all of the reactants are unknown, the prediction of the course of photosynthesis is relatively easy because of the lack of restrictions on the choice of assumptions.

ORNSTEIN, who investigated (1938) the relations between chlorophyll fluorescence and photosynthesis in *Chlorella* cells, arrived at the conclusion that chlorophyll is only active in the absorption and transfer of light energy to reacting molecules, but is not linked to chemically active molecules in the Blackman reaction.

Products of the mechanism:- The first and foremost attempts to depict the genesis of carbohydrates were made by chemists. LIEBIG formulated (1843) a concept that they were formed by a series of steps showing successive decreases in the amounts of oxygen in the compounds formed and an increase in the amount of hydrogen. For example, carbonic acid might be reduced to oxalic, then to tartaric, malic and other fatty acids. This idea that organic acids are intermediate stages in the production of carbohydrates, though never proven, has been expressed subsequently by other writers, and among them were some who suggested that formic acid was the first reduction product. The idea that formaldehyde is the first stage in the formation of carbohydrate has commanded more attention.

The credit for formulation of the formaldehyde theory usually goes to BAEYER who, in 1870, advanced the theory that sugar might be formed from formaldehyde by a process of polymerization. It was generally admitted that polymerization may be comparatively readily induced, but convincing evidence that formaldehyde is actually produced by the assimilation of CO_2 was not readily obtained. BALY, HEILBRON, and BARKER reported (1921) that sugar was formed by exposing a solution of formaldehyde to ultraviolet light. They added calcium carbonate to the solution and found that the maximum reducing power was about 8 percent, calculated as glucose. SPOEHR failed, however, to obtain confirmatory results, although he exposed 3 percent solutions of formaldehyde in flasks to strong sunlight for as long as four months. In answer to criticisms, BALY stated (1922) that ordinary formaldehyde is not condensed to sugar under most conditions but that the formaldehyde molecule produced in the process of photosynthesis is in a highly reactive state, designated by him as "activated formaldehyde". The number of works on the alleged formation of formaldehyde *in vitro* from carbonic acid is exceedingly great; but many of them have but little reference to the biology of the process, in fact some of the proposed reactions would have wrecked the metabolism of any plant.

The study of carbohydrate metabolism followed apace on the discovery of the salient features of carbon fixation. A few observations upon the subject must suffice for the present discussion. Many carbohydrates are utilized or accumulated, or changed from one form into another. Consequently there is a constantly changing and often complicated interplay between the products arising from the process of carbon fixation in the plant.

The way for investigations on carbohydrate transformations in plants was opened in 1862 by SACHS, whose work led him to the conclusion that starch is the first product of photosynthesis and that it occurs in the plastid. In the succeeding decades the problem was investigated by many workers and important discoveries were made. Some notable exceptions to SACHS' conclusions were found; in fact BOEHM had earlier observed (1857) that normal chloroplasts of species of *Allium, Galanthus,* and other plants did not contain starch.

SCHIMPER arrived (1885) at the conclusion that it was possible that glucose was a preliminary product and that starch only appeared after the glucose had reached a certain concentration in the cells. Since the point of equilibrium could differ in different

plants, SCHIMPER believed that under normal conditions many plants never reach the stage of starch formation, while in others it is regularly reached and starch is formed.

SAPOSCHNIKOFF demonstrated (1889) that starch was formed in leaves normally starch-free when they were supplied with sucrose. WINKLER later showed (1898) that, with few exceptions, all chloroplasts and leucoplasts could form starch if the leaves were floated on sucrose solution. BROWN and MORRIS, who examined (1892) the leaves of various plants, found sucrose, maltose, glucose, and fructose and came to the surprising conclusion that sucrose, in the leaves of *Tropaeolum,* was the first sugar to be synthesized by the assimilatory process. They regarded sucrose as the starting-point of all the metabolic changes taking place in the leaf, functioning first as a temporary reserve material and eventually accumulating in the cell sap of the leaf parenchyma. Excess of sucrose was converted into starch, while for purposes of translocation sucrose was converted to glucose and fructose.

PARKIN, who worked (1911) on *Galanthus,* also concluded that sucrose was the sugar first formed in the leaf. In a later discussion in 1925 he suggested that the equilibrium in the plant may be

$$\text{Starch} \rightleftarrows \text{glucose} \rightleftarrows \text{sucrose.}$$

When starch-free leaves were fed with sugar solutions sucrose proved to be a better former of starch than invert sugar. Since these two carbohydrates are so intimately connected, he felt warranted in calling sucrose the precursor of starch. DAVIS, DAISH, and SAWYER studied (1916) the metabolism of carbohydrates in the mangold leaf and, while they found no maltose in the leaf, they found that sucrose was always in excess of glucose and they also concluded that sucrose was the first product of carbon fixation. PRIESTLEY advanced (1924) the idea that, since sugars are transitory substances, they pass rapidly into other substances in the complex chain of metabolic changes instead of accumulating in the light and therefore fluctuate in amount. Accordingly hexose, when its concentration reaches a certain point, is converted into sucrose. He believed that hexoses, and not sucroses, are the primary photosynthetic sugars.

New light upon the subject was supplied in 1924 by WEEVERS, who compared the sugar content of the green and non-green portions of variegated leaves of a number of plants. In most of them he found both sucrose and hexose in the green, but only sucrose in the non-green portions. In other cases hexose in small amounts as well as sucrose was found in the non-green portions. Results of a dissonant nature have been subsequently obtained by others.

The transport of sugars from leaves was easily demonstrated, but the movement of starch presented difficulties. MEYER assumed (1895) that a diastase was formed in the stroma of the chloroplast, but could not extract such an enzyme by pressing the sap of macerated leaves. BROWN and MORRIS (1893) dried the plants at 40° to 50°C. and showed that the powder obtained by pulverizing the dried tissues exhibited enzymatic activity.

When it was established by SCHIMPER's brilliant researches in 1880 that starch is not only a product of photosynthesis but a form of stored energy of the plant, the last great advance in carbohydrate metamorphosis was made. Countless memoirs have since

appeared in which a myriad of details have been studied, but no comparable advance has been made.

The study of the conversion of soluble carbohydrates into all-important cellulose has been consistently neglected by physiologists and chemists alike. As indicated in the chapter on cytology, cellulose is formed by the activity of an adjacent layer of cytoplasm which is in turn bathed by cell sap (a solution of raw materials).

An important theory of the mechanism of cellulose formation by the deposition of glucose residues was formulated (1929) by SPONSLER, which is consistent with the idea that the deposition of new material is made at the interface between the cytoplasm and the wall and that glucose is transformed directly into cellulose. From X-ray studies SPONSLER found that the regular arrangement of the structural units of the cell wall is essentially the regularity of crystal structure. The glucose residues are not only spaced in an orderly manner, but are oriented in a definite way with respect to one another, from which he concluded that forces are involved in locating and orienting the residues in the cell wall which are comparable to those acting in a similar way on the sugar molecules during the formation of a sugar crystal. The inner face of the cell wall may consequently be considered as similar to a crystal face as regards the distribution of forces involved in the deposition of new lattice units. The particular structure of the glucose molecule seems to provide an opportunity for a condensation reaction which would produce long straight chains of residues, or cellulose molecules. He pointed out that there must be another factor in the transformation of glucose to cellulose, which is associated with some reaction which can only occur when living protoplasm is present. Since growth of the cell wall may be localized on one particular face, SPONSLER concluded that the factor determining deposition is localized in the cell.

BROWN and MORRIS showed (1890) that the cellulose which the plant produces may in some cases be reconverted into soluble substances and utilized as a source of energy. They demonstrated that the dissolution of the cell walls of the endosperm of a seed during germination is caused by enzymic action.

E. SCHULZE, in his studies published from 1889 to 1892, designated a group of substances in plant cell walls as hemicellulose, and showed that they often served as a reserve supply of carbohydrate. It appears from his work that in cell walls there are various polysaccharides which can be hydrolyzed with dilute H_2SO_4 with the formation of mannose, galactose, arabinose, and xylose. The original term hemicellulose thus came to include a rather heterogeneous collection of substances in the cell wall, including mannosans, galactosans, and pentosans which are the anhydrides of the corresponding sugars.

GRÜSS showed (1897) that the hard endosperm of date seed yielded upon hydrolysis mannose. NEWCOMBE found (1899) that the hemicellulose compound which is important in certain organs will be attacked by specific cytases. Although he was unable to separate those enzymes from diastase he could show a differential action which distinguished the amylolytic from the cytolytic activities. TOTTINGHAM (1921) and MURNEEK (1929) investigated the reserve hemicelluloses of fruiting branches of apple trees. They interpreted their results as strong evidence that these substances

are important as reserve carbohydrates. Hemicelluloses, according to MURNEEK, made up 17 to 22 percent, while starch was only 1 to 4 percent of the dry weight. E. SCHULZE analyzed (1896) seeds of lupine in the dry and germinated states, and concluded that the galactan obtained from them must be a reserve material, since it disappeared during the process of germination. BERNARDINI and GALLUCIO, however, found (1912) that during germination in light, pentosans increased; though during germination in darkness they increased very little. A clear-cut decision about the physiological rôle of hemicelluloses is difficult to formulate, since the literature on the subject contains many discordant statements. The concept that they form a chemically distinct group has been abandoned.

Chemosynthesis by bacteria:- The foregoing discussion of the photosynthetic assimilation of CO_2 by green plants must be supplemented by some consideration of the same process in the photosynthetic bacteria. The process, although not known until the latter part of the 19th century, indicates that the constructive power of protoplasm is greater and more varied than was theretofore assumed by botanists.

ENGELMANN, who was the first to formulate (1883) a concept of the photosynthetic power of the purple sulfur bacteria, was unfortunately mistaken about some fundamental things, due to faulty technique. He demonstrated, however, that the purple bacteria develop best in bright light.

The important discovery in this field was made by WINOGRADSKY in 1887 when he found that the colorless sulfur bacteria in the absence of light can oxidize H_2S and S to sulfuric acid. He found that they not only maintain themselves on energy derived from this oxidation, but are also capable of reducing CO_2 in the dark at the expense of this energy. He formulated at that time the important concept of chemosynthesis, designating therewith the particular type of metabolism in which the organisms utilize the energy derived solely from the oxidation of H_2S without the aid of solar energy. WINOGRADSKY maintained cultures of the filamentous sulfur bacteria under a cover glass in a moist chamber in order to obtain an insight into their physiology. The water in which they were mounted contained H_2S. By continual renewal of the water, he succeeded in keeping *Beggiatoa* living for weeks while making microscopical observations. He assumed correctly that the *Beggiatoa* were able to utilize CO_2 as a source of carbon with energy made available by the oxidation of H_2S. The process was stated later as

$$CO_2 + 2H_2S = HCOH + H_2O + S_2$$

WINOGRADSKY saw and depicted the sulfur granules which accumulated in cells of the bacteria under experimentation, emphasizing that the sulfur came from the H_2S furnished. The energy for the organisms comes from the oxidation of H_2S, without which they cannot long survive.

The purple sulfur bacteria can also oxidize H_2S and S to sulfuric acid and the idea was advanced that these organisms would be chemosynthetic.

MOLISCH undertook to study the purple bacteria with which ENGELMANN had experimented. He concluded (1907) that those

organisms were not autotrophic, but that light enabled them to assimilate organic compounds, and he denied the evidence obtained by WINOGRADSKY that H_2S is necessary. It took some time for the minds of men to comprehend the nature of chemosynthesis in bacteria, and there were subsequent attempts to uphold MOLISCH's erroneous idea. SKENE adopted a better technique than his predecessors and found (1914) that these organisms can grow in a purely mineral medium containing H_2S under almost anaerobic conditions.

MOLISCH had considered that the sulfur-bearing (*Thiorhodaceae*) and the sulfur-free purple bacteria (*Athiorhodaceae*) were fundamentally similar, because he thought that both required organic matter for their development. The former are, however, true autotropic organisms since (as WINOGRADSKY reported) they can construct their own cell components. The process has been assumed to be:

$$CO_2 + \tfrac{1}{2}H_2S + 2H_2O = HCOH + H_2O + \tfrac{1}{2}H_2SO_4$$

The phenomenon of chemosynthesis was extensively studied by VAN NIEL, who concluded (1931) that the purple and green sulfur bacteria are truly photosynthetic organisms. Under favorable conditions the purple sulfur bacteria dehydrogenate hydrogen sulfide, sulfur, sulfite, and thiosulfate completely to sulfate with a corresponding reduction of CO_2. However, in the absence of oxidizable sulfur compounds, these bacteria can develop in the presence of organic compounds under completely anaerobic conditions if there is a simultaneous supply of radiant energy. The sulfur-free purple bacteria (*Athiorhodaceae*) under aerobic conditions seem to be independent of light, but under anaerobic conditions light is necessary. The same author concluded (1935) from a large body of evidence produced by various workers that the fundamental photosynthetic process in the sulfur bacteria in organic media is one of the general type

$$CO_2 + 2H_2A \xrightarrow{\text{light}} (HCOH) + H_2O + 2A$$

in which H_2A, the H-donor, is represented by a variety of simple organic substances.

REFERENCES:-

BOEDLER, J. (1927): Die Kohlensäureassimilation, ein Sammelreferat. Bot. Arch. 20:143-178.

BRIGGS, G. E. (1933): Induction phases in photosynthesis and their bearing on the mechanism of the process. Proc. Roy. Soc. (London) ser. B, 113: 1-41.

BROWN, H. T. and ESCOMBE, F. (1905): Researches on some of the physiological processes of green leaves, with special reference to the interchange of energy between the leaf and its surroundings. Proc. Roy. Soc. (London), Ser. B, 76:29-111.

EMERSON, R. (1937): Photosynthesis. Ann. Rev. Biochemistry 6:535-556 (with bibliography).

HOTTES, C. F. (1932): The contributions to botany of Julius von Sachs. Annals Mo. Bot. Garden 19:15-30.

MARCHLEWSKI, L. (1909): Die Chemie der Chlorophylle und ihre Beziehung zur Chemie des Blutfarbstoffs. 2te Aufl. Vieweg, Braunschweig.

MEYER, A. (1883): Das Chlorophyllkorn in chemischer, morphologischer und biologischer Beziehung. Felix, Leipzig.

PRIESTLEY, J. H. (1924): The first sugar of photosynthesis and the role of cane sugar in the plant. New Phytologist 23:255-265.

PRINGSHEIM, E. G. (1932): JULIUS SACHS. Fischer. Jena.

ROTHMUND, P. (1935): Protochlorophyll. Cold Spring Harbor Symposia on Quant. Biol. 3:71-79 (bibliography).

SACHS, J. (1862): Über den Einfluss des Lichtes auf die Bildung des Amylums in den Chlorophyllkörnern. Bot. Zeit. 20:365-373.

—— —— (1864): Über die Auflösung und Wiederbildung des Amylums, u.s.w. Bot. Zeit. 22:289-294.

SCHIMPER, A. F. W. (1885): Über Bildung und Wanderung der Kohlehydrate in den Laubblättern. Bot. Zeit. 43:737-743, 753-763, 769-787.

SCHUNCK, E. (1889): The chemistry of chlorophyll. Annals of Bot. 3:65-121.

SPOEHR, H. A. (1926): Photosynthesis. Chemical Catalog Co., New York.

SPONSLER, O. L. (1929): Mechanism of cell wall formation. Plant Physiol. 4:329-337.

STILES, W. (1925): Photosynthesis. Longmans Green, London (with bibliography).

VAN NIEL, C. B. (1935): Photosynthesis of bacteria. Cold Spring Harbor Symposia on Quant. Biol. 3:138-150.

WILLSTÄTTER, R. and STOLL, A. (1913): Untersuchungen über Chlorophyll. Springer, Berlin. (Eng. transl. by SCHERTZ, F. M. and A. R. MERZ 1928, Science Press, Lancaster, Pa.).

WINOGRADSKY, S. (1887): Zur Morphologie und Physiologie der Schwefelbakterien. Bot. Zeit. 45:493, 513, 529, 545, 569, 585, 606.

Chapter XIV.

THE ASSIMILATION OF NITROGEN.

In the early years of the nineteenth century there were no sound concepts of the origin and assimilation of nitrogen. Men knew that living beings contained appreciable amounts of nitrogen, and that some of it returned to the soil, but they were ignorant of any means for maintaining an adequate supply of soil nitrogen. DE SAUSSURE's brilliant researches had afforded him no convincing evidence on the problem. He knew that plants acquired nitrogenous material from animal or vegetable matter, or from such ammoniacal vapors as they may find in the soil or extract from the air. He was convinced that plants cannot grow normally without a suitable source of nitrogenous material, but further than that he did not go.

The peculiar value of clover and other legumes for soil enrichment had been known since the days of the Romans, but at the beginning of the nineteenth century opinions differed as to the reason. When it was realized that the atmosphere contains much, and the soil little, nitrogen, it was natural to attempt to discover some way by which plants could lay hold on atmospheric nitrogen. LIEBIG, who had controverted, partly by scientific evidence and partly by polemics, the idea that plants could obtain their carbon from soil humus turned his attention to nitrogen nutrition. He concluded (1840) that the nitrogen of the plant likewise comes from the atmosphere and abandoned the idea that plants obtain nitrogen from humus, citing experiments in which plants grew perfectly well in a mixture of charcoal and earth (previously calcined) if supplied at the same time with rain water. With a logic supremely reminiscent of medieval scholastics, he proceeded to argue that the nitrogen taken by the plants is ammonia, which may come from the soil, from organic manures, or from the air.

LIEBIG was very positive that ammonia is, and was, the sole source of nitrogen for plants, stating that "Science is at present ignorant of any compound of nitrogen besides ammonia capable of yielding nitrogen to wild plants on all parts of the earth's surface . . . and therefore, until a second source of nitrogen is discovered, we must, in science, view ammonia as the *only* source". He thought that all plants are able to secure their nitrogen from the air, and that legumes and other broad-leaved plants excelled in that power. His conclusion rested on the fact that legumes are less responsive to nitrogenous fertilizers than cereals and also that cereals grow better when a leguminous crop precedes.

LIEBIG deserves credit for his demonstration that the green plants utilize only combined nitrogen. His opinion that the ultimate source of the combined nitrogen is the ammonia of the atmosphere was not, however, accepted by all the contemporary scientists. It was soon demonstrated by investigations on the Continent and in England that the amounts of ammonia and of other nitrogenous

compounds in the air are very small, and that the amounts brought down in the rain or snow would account for only a small part of the nitrogen found in crop plants.

Early work on the acquisition of nitrogen by plants:- The way out of the darkness which overspread the question of nitrogen assimilation was found eventually not by physiologists, but by chemists, who were interested primarily in agriculture. Peradventure there were at the beginning of the nineteenth century experienced farmers whose opinions were nearer the truth than either the chemists' or the physiologists'.

BOUSSINGAULT undertook experiments on the acquisition of nitrogen by plants. In 1837 he grew a pot of *Trifolium* for two months and another for three months in calcined soil watered with distilled water and with the access of free air; also a pot of wheat for two months and another for three months. The total nitrogen in the seed sown in the two experiments with *Trifolium* amounted to .224 gram. When the experiment was terminated, the nitrogen in the produce, soil, pot, etc. amounted to .276 gram. There was a gain, therefore, of .052 gram of nitrogen, or nearly 20 percent of the total nitrogen of the product. In the two experiments with wheat, the total nitrogen in the seed was estimated at .100 gram. The nitrogen in the product was exactly the same amount. In the case of wheat there was, therefore, no gain of nitrogen indicated. Nevertheless the dry matter of the produce amounted to nearly double that of the seed. From the above experiment he concluded that certain plants seemed adapted to take up nitrogen from the atmosphere, but it was still a question under what circumstances and in what state the nitrogen was fixed in the plant. He conceived that the nitrogen might enter directly into the plant, provided its green parts were adapted to fix it; that it might be conveyed into the plant in the aerated water taken up by its roots; or that the atmosphere contained an infinitely small amount of ammoniacal vapor. Having found gains in the nitrogen of the soil-plant system in excess of the amount furnished in the manures, he speculated about its source. Since it evidently came from the atmosphere, he thought it might have been formed by electrical action and carried down as nitrate of ammonia by rain.

BOUSSINGAULT continued his experiments many years later, using more refined methods. In his experiments in 1851 and 1852, plants were grown under a glass jar of about 35 liters capacity, which rested in a bath of sulphuric acid. Tubes passed under the edge of the bell jar for the supply of carbonic acid and water as they might be needed. The medium in which the roots grew consisted of pumice stone, coarsely powdered, washed, ignited, and cooled over sulphuric acid. Some of the ash from farmyard manure and also from seed of the kind to be sown was added. He found that when the leguminous plants grew under these conditions in which the free circulation of atmospheric air was not permitted, there was not the apparent gain of nitrogen that had been met with in his early experiments. Oats grown under similar conditions showed a very slight loss of nitrogen. In 1853 he utilized a large carboy of white glass, having a capacity of 70 or 80 liters, into which he placed pumice stone with ashes prepared as in the previous series. This was watered with distilled water and then

the seeds were sown. The necks of the vessel were then closed with a cork. Through a perforation in it, a flask of carbonic acid was inverted. Access to the outside air was excluded by rubber bandages. In this, as in the last case, he found that there was no gain in the nitrogen content of lupines or beans.

In 1855 and 1858 BOUSSINGAULT made experiments on the action of nitrates upon vegetation by growing sunflowers in two separate pots, each of which contained ignited sand and quartz previously washed to remove saline material. One pot received .0111 gram of nitrogen in the form of potassium nitrate, and the other .022 gram. After the plants had grown, they were dried and analyzed. In the first case, he did not get back in the plant, soil, and pot the nitrogen of the seed and added nitrates by .0014 g. In the second case, the loss of nitrogen amounted to exactly 1 milligram. He found, however, that there remained in the soil an amount of potassium carbonate very nearly corresponding in potassium to the amount of potassium nitrate which would represent the observed loss of nitrogen. From this he concluded that nitrates had been decomposed in the soil by the organic matter of the debris of the seeds and of the roots, and that nitrogen had been evolved.

VILLE, who also made important experiments, utilized pots containing soil washed and ignited, sand, sand and brick, or sand and charcoal, with the addition of the ash of the plant to be grown. The pots were for the most part enclosed in a glazed case, through which a current of air equal in amount to several times the volume of the vessel was drawn daily. Carbonic acid and distilled water were supplied as needed. In 1849 three crops of plants were grown in sand for two months: namely, one of cress, one of large lupines, and one of small lupines. The air admitted into the apparatus was not previously deprived of its natural ammonia. The nitrogen found in the cress plants amounted to .147 gram, in the original seed to .026 gram. In the case of the large lupines the dry matter of the produce was about three and one-half times as great as that of the seeds sown, but there was neither gain nor loss of nitrogen. The small lupines gave two and one-half times as much dry substance in the produce as was supplied in the seeds, but there was an apparent loss of rather more than one-fourth the nitrogen during the experiment. The total gain of combined nitrogen in the apparatus, taking the three crops together, was .103 gram. The nitrogen in the ammonia of the current of unwashed air was, however, estimated at only .001 gram. M. VILLE concluded, therefore, that the cress had appropriated a considerable quantity of the free or uncombined nitrogen of the atmosphere, but he said nothing about the loss noted in the case of the lupines.

Experiments were also made with a current of air washed free from ammonia. In every case the dry matter of the produce was many times that of the young plants or seeds. In the case of the sunflower it was more than one hundred times that of the seeds. In each experiment there was a gain of nitrogen. In the experiment with autumn colzas there was 4.7 times, in that with spring wheat 2.2 times, in that with sunflower 25.5 times, in one with summer colzas 3.4 times as much nitrogen in the total product as in the original plant or seed. The total amount of nitrogen gained in

the five experiments was 1.624 grams, which was 5.3 times as much as was contained in the total original plants and seeds, although the air circulating through the chamber had been drawn over pumice stone saturated with sulphuric acid to remove the ammonia which it carried.

M. VILLE decided from his experiments that plants can take up nitrogen in three forms, namely as nitric acid, as ammonia, and as free nitrogen, enumerating the following conclusions:

"1. By means of niter we may prove without the aid of an enclosing apparatus that plants absorb and assimilate the gaseous Nitrogen of the atmosphere. 2. Niter acts by its nitrogen. It is absorbed in the state of niter. 3. In relation to the amount of nitrogen, niter is more active than ammonium salts".

It will thus be seen that results obtained by VILLE were somewhat at variance with those obtained by BOUSSINGAULT on the utility of different forms of nitrogen for plants.

While pioneer work was being done in France on the question of the nitrogen nutrition of plants, a related line of work was going on in Britain. There was published in the Philosophical Transactions of the Royal Society for 1861 an elaborate account of experiments conducted by LAWES, GILBERT, and PUGH. These men were interested in ascertaining the sources of the nitrogen of vegetation and profited by the earlier work of BOUSSINGAULT and VILLE. Unfortunately the growth of the leguminous plants in their closed apparatus was far less satisfactory than that of the cereals. At the conclusion of their report they said that their experiments on the question of assimilation did not favor the supposition that there was any loss of combined nitrogen due to the evolution of free nitrogen from the plants during growth.

In numerous experiments with cereals grown with and without a supply of combined nitrogen beyond that contained in the seeds sown, they found no evidence of an assimilation of free or uncombined nitrogen. The growth of leguminous plants was less satisfactory and the conditions in their experiments favorable for the assimilation of free nitrogen was therefore more limited. So far as they went, however, their results did not indicate to them any assimilation of free nitrogen.

We now know that there could be no assimilation of free nitrogen by the symbiotic bacteria because they had previously sterilized the soil or the pumice stone in which the seeds grew. After a long account of their experimental work, they concluded that free nitrogen is not assimilated by plants under the wide range of conditions provided in their experiments. Nevertheless, they recommended that the several actual or possible sources of combined nitrogen to plants should be more fully investigated. This was done many years later and the results were reported at a meeting in Berlin at which Dr. GILBERT was present.

Ammonification:- The fundamentally important functions of microorganisms in the formation of ammonia from soil organic matter were discovered some time after the science of microbiology had been established. The role of bacteria was suggested when MÜNTZ and COUDON showed (1893) that the process of ammonification was stopped by sterilizing the soil. Simultaneously MARCHAL studied (1893) the organisms which form ammonia from the pro-

teins of plant residues or of animal manures. He concluded that *Bacillus mycoides* was an important ammonia producer in the soil, but that various fungi were significant in acid muck soils.

The original idea that ammonia production is due principally to the well known spore-forming bacteria was considerably modified by later studies. CONN discovered (1919) that *Ps. fluorescens* and other non-spore forming organisms rapidly increase in manured soil and produce ammonia from stable manure. The rate of ammonia formation depends upon conditions, but effective microorganisms are almost never absent according to REMY (1902) and LÖHNIS (1906). The amounts of ammonia present in the soil at any one time according to RAMANN (1911) may be between 0.0005 and 0.002 percent.

LATHROP found (1916) that the ammonification of dried blood in a sandy loam soil was rapid during the first 86 days, after which the rate decreased rapidly. Four-fifths of the nitrogen of the dried blood was converted into ammonia nitrogen during the 240 days that the observations were made.

Ammonia as a nutrient:- Information on the assimilation of ammonium salts by plants is scanty in spite of the subsequent researches on its formation and occurrence in soils. LAWES and GILBERT's classical experiments with fertilizers included ammonium salts, but afforded meager information about their value as plant nutrients since the ammonia added to the soil does not remain long until nitrification processes convert it into nitrites and nitrates.

MAZÉ concluded (1900) that ammonium salts were as favorable for the growth of maize as nitrates, provided the concentration of the former was low. In later stages of development, however, nitrates were more favorable.

STAHL and SHIVE also observed (1933) that absorption of ammonia and nitrates by oats and buckwheat is dependent upon the age of the plant. In the earlier stages of growth those plants absorbed ammonia most rapidly, but later, at the time of flowering, they absorbed less ammonia and more nitrate.

RUSSELL pointed out (1917) that, although comparisons between the nutritive values of ammonia and nitrate are difficult to interpret because of the action of bacteria, it has been shown definitely that ammonia is readily assimilated from weak solutions of ammonium sulphate. GERLACH and VÖGEL grew (1905) maize in carefully sterilized solution-cultures and reported that the plants in the ammonium solutions were as good as those in nitrate. KRÜGER who studied the nitrogen nutrition of a number of plants reported (1905) that ammonium sulphate and sodium nitrate were equally useful for oats, barley, and mustard; ammonium sulphate was better for potatoes and less favorable for mangolds. HUTCHINSON and MILLER found (1909) that nitrates produced better growth of wheat, and that both forms of nitrogen were equally beneficial to peas.

PRIANISCHNIKOV, who devoted many years to the investigation, maintained that ammonium salts have specific beneficial effects upon plants. He and his pupils studied (1924 and 1926) the relative values of nitrates and ammonia for plants grown in water cultures and concluded that the utilization of ammonium salts

depends upon the amount of carbohydrate present and upon the hydrogen-ion concentration of the medium. He believed that plants absorb ammonia in preference to nitrate because the latter must be reduced to ammonium compounds within the plant before the nitrogen can be utilized. The involved explanations which PRIANISCHNIKOV gave concerning the mechanism of ammonium utilization are not, however, very satisfying to the reader. He admitted that, under natural conditions in a well aerated soil, nitrifying organisms would continually convert ammonium into nitrate nitrogen where bases favorable for the growth of the higher plants occur, whereas ammonia is likely to be formed in poorly aerated soils and where mineral complexes incompletely saturated with bases occur.

PRIANISCHNIKOV reported (1929) that sugar beets took up more ammonia than nitrate at *p*H 7.0, but that the relations were reversed at *p*H 5.0. The findings of others on this question are not concordant. For example, ARRINGTON and SHIVE reported (1935) that at *p*H 4.0 the ratio of ammonia to nitrate absorbed was 4.7 while at *p*H 7.0 it was 1.2.

HOAGLAND pointed out (1932) that ammonium salts are more apt to be injurious to plants than nitrates unless temperature, illumination, and hydrogen-ion concentration are carefully adjusted. He found that when nitrogen was furnished as ammonium compounds the rate of nitrogen absorption increased with an increase of *p*H. MCKEE called attention to the importance of the carbohydrate supply in the utilization of ammonia, stating (1937) that the ammonium ion which is toxic must be converted into innocuous organic compounds. ARNON discovered (1937) an important relation of manganese to ammonia utilization.

Nitrification:- Nitrification in soil humus or in other substance was investigated in a somewhat haphazard fashion until after the establishment of a science of bacteriology. Prior to that time nitrification was considered as a purely chemical reaction resulting from the oxidation of the gaseous nitrogen of the air in the soil, or in the compost heap. It is true that BOUSSINGAULT demonstrated that soil nitrates are formed from humus nitrogen and not from nitrogen gas, but neither he nor any of his contemporaries considered that it was anything but a purely chemical process. The first recorded suggestion that microörganisms might cause nitrification came in 1862 from PASTEUR in the form of a recommendation that everything which pertained to nitrification should be re-examined in the light of the germ theory. It was sixteen years later that two French investigators, SCHLÖSING and MÜNTZ, adduced proof of the necessity of biological factors in nitrification. These men were interested in discovering a method for rendering the effluents of the Paris sewers innocuous for irrigating fields at Gennevilliers near Paris.

SCHLÖSING and MÜNTZ found (1877) that when diluted sewage trickled through long glass tubes filled with soil it lost its ammonia and gained an equivalent quantity of nitrate after the experiment had run about 20 days. They passed chloroform vapor into the contents of some actively nitrifying tubes and found that nitrification was at once inhibited. The process could be re-established, however, by adding an infusion of garden soil to the contents of

the tubes. They also showed that nitrification could be stopped by heating the tubes to 100°C. Their conclusions that the process was the result of microbial activities were soon confirmed by many other workers, but the isolation and identification of the organisms were difficult problems. There were two inherent and unsuspected reasons for the failures of the first attempts, namely, the associative character of the nitrite and nitrate bacteria and the unsuitability of rich bouillons and gelatin media for the organisms.

WARINGTON, who conducted researches at the Rothamsted Station from 1878 to 1891, obtained the first definite evidence that two groups of microbes must coöperate in nitrification. One group produces only nitrites, and the other only nitrates. Professor and Mrs. Frankland reported (1890) that they had isolated the microbe, but the pure cultures did not produce nitrates.

WINOGRADSKY's epoch-making work was in progress at this time and he soon discovered the salient facts about nitrification. He succeeded in isolating the two groups of microbes responsible for the oxidation of ammonia to nitrate; the first produced nitrites from ammonia, the second produced nitrates from nitrites. The first are oval, and the second are small rod-shaped organisms. He named the oval nitrite-formers *Nitrosomonas,* and the small rod-shaped nitrate-formers *Nitrobacter.* Having shown (1890 and 1891) that the nitrifying organisms do not develop on media suited to other bacteria, he ingeniously devised media containing only inorganic salts and replaced gelatin with silica jelly. The two-fold nature of the natural nitrification process was soon thereafter confirmed by WARINGTON, MÜNTZ, HALL and others.

The discovery of the nature of the process of nitrification had great scientific and practical importance since it is apparent that most of the nitrogen used by plants is taken up in the form of nitrate. It also showed the significant role of bacteria in the nitrogen cycle in nature. WINOGRADSKY's discovery of the physiology of the nitrite bacteria went hand in hand with his elucidation of the process of chemosynthesis already outlined in the chapter on carbon fixation. For the first time he demonstrated that certain bacteria could grow and make normal development in media which contained no trace of organic material, either in light or in darkness, utilizing the carbon dioxide of the atmosphere. His experiments demonstrated that the energy employed in the formation of carbon compounds is derived from the oxidation of ammonia.

The influence of water, temperature, and other factors of a physico-chemical nature upon nitrification have been extensively studied but will be omitted from the present discussion, except to mention the annual periodicity. LÖHNIS established (1905) that at Leipzig there were two maxima, one in the spring, the other in the fall, and two minima, in midsummer and winter. KING and WHITSON (1900) and C. A. JENSEN (1910) found the maximum production in the northern United States in the spring. MÜNTZ and GAUDECHON reported (1912) that the maximum nitrification occurred in France from February to the middle of April. RUSSELL suggested (1914) that the summer minimum is due to the activities of protozoa and other soil organisms unfavorable to the nitrifying bacteria, though later work did not verify the hypothesis.

Nitrates as nutrients:- BOUSSINGAULT's experiments previously mentioned had shown the value of nitrates as a source of nitrogen for higher plants, but his contemporaries were slow in adopting the idea. Imbued as they were with the dogma that ammonia is the chief source of combined nitrogen for the plant, they assumed that the nitrate added to the soil must first be transformed into ammonium compounds.

BOUSSINGAULT opposed (1860) this assumption, believing that the nitrate as such is absorbed by the plant. He obtained undoubtedly greater growth from the application of nitrate, though it is now recognized that his experimental methods were not technically perfect. DE CANDOLLE had shown (1832) earlier that nitrates occur in a very large number of phanerogams and since his time the list has been extended. VILLE had been very positive that nitrate was more active than an equivalent amount of nitrogen in the form of ammonia, supporting BOUSSINGAULT's thesis.

Interpretations of some of the early work in this field are difficult because the workers could not know that changes and conversions of the nitrogen compounds were being continuously wrought by bacteria. The compounds which the plants acquired were usually different from those which the experimenter applied.

The increased use of nitrates in agriculture stimulated the use of Chilean nitrate. The deposit of Chilean nitrate of soda which has been so largely used in agriculture was discovered accidentally by NEGREIROS, a wood cutter. Having built a fire of wood, he was surprised to see the earth around his fire flash and sputter, then to melt and run like a liquid flame. The use of nitrate of soda as a fertilizer was promoted by the methods for partial purification developed by THADDEUS HAENKE, a naturalist on the Malaspina expedition which visited the west coast of South America in 1788. The first exportations of nitrate were made to England about 1820 and the substance was increasingly employed in agriculture after 1831, until modern methods of nitrogen fixation superseded to a large extent the Chilean nitrate.

HELLRIEGEL and associates studied the relation of nitrates to the growth of barley through a number of years, utilizing sand cultures and providing optimum conditions for the plants. They showed (1897) a dominant effect of the nitrate added to the sand cultures. Where no nitrate was added, the plants had at their disposal only the nitrogenous compounds in the parent seed. The addition of very small amounts of calcium nitrate produced relatively great increases in the production of grain and straw. From the time that LAWES and GILBERT initiated their experiments the effects of ammonium compounds and nitrates upon plant growth were carefully studied. They confirmed much that BOUSSINGAULT had reported, *i.e.*, nitrates produced greater vegetative growth. The leaves usually developed a dark green color and attained maximum size. RUSSELL emphasized (1932) the desirable effects of nitrates as a source of nitrogen on crops which are grown for their vegetative organs and, contrariwise, the possibility that the maturity of wheat and other cereal crops might be so delayed by the action of nitrates that the crop would be injured by frost. WALLACE described (1923) the effects of nitrogen deficiency on apple trees, *e.g.*, early abscission of leaves, death of lateral buds, reduction of root system, and abnormal color of fruits. Addition

of nitrate to supply a deficiency caused a rapid improvement in color and growth of the leaves.

The amounts of nitrate to be found in the plant are relatively small according to various investigators since the time of LIEBIG. MOLISCH showed (1913) that varying conditions determine the amount of nitrate present in the organs of the plant. Investigators generally concluded with the perfectly naive statement that the amounts were small where the utilization or conversion was rapid. SCHIMPER's meritorious work, on the contrary, elucidated (1890) some important aspects of the nitrate partition phenomenon, showing that an especially rapid nitrate decomposition occurs in illuminated green leaves, but not in the white areas of "variegated" leaves nor in the chlorophyll-free aerial roots of *Tradescantia.* He also reported that shade-leaves were richer in nitrate than sun-leaves.

The effect of the carbon/nitrogen ratio in the plant which was discussed by KRAUS and KRAYBILL in 1918 attracted attention from many writers. KRAUS and KRAYBILL found that the flowering and fruiting of the tomato only occurred when the carbon/nitrogen ratio varied within a comparatively narrow range. Although a certain relation may exist in annuals like tomatoes, HOOKER and BRADFORD who studied (1921) the localization of factors concerned with fruit-bud formation on apple trees saw no significance in the carbon/nitrogen ratio.

Other sources of nitrogen as a nutrient:- The role of organic nitrogen compounds in plant nutrition has often been discussed. The incorporation of barn yard manure, of guano, of urea with the soil, to say nothing of plant detritus aroused interest in the question in the last century. KNOP and WOLF found (1865) that the addition of glycocoll, tyrosin, and leucin resulted in protein formation in cereals grown in water cultures, while other compounds were either indifferent or toxic. In the earlier experiments the possibility of bacterial action was not precluded. BAESSLER attempted (1887) to obviate the difficulties by culturing maize plants in a N-free medium, and transferring them for a few hours daily into an asparagin solution; through which he succeeded in showing that there was an intake of N and an increase in protein at the expense of the asparagin supply.

SCHREINER and SKINNER, who made an extensive investigation of the effects of nitrogenous soil constituents on plant growth, reported (1912) that nucleic acid, xanthine, guanine, creatinine, and other compounds had a beneficial effect upon plant growth in water cultures. Their chemical control showed that there was no decomposition of the compounds employed to ammonia, nitrite, or nitrate, on the contrary the plants absorbed and used them (or were poisoned by them). The beneficial effects were less marked where nitrate was also present. Guanidine was harmful and produced singularly specific effects upon the leaves. In the presence of nitrates the harmful effect was greater and in their absence it was least conspicuous. HUTCHINSON and MILLER concluded (1911) that for peas growing in germ-free cultures some organic nitrogen compounds were useful as sources of nitrogen, while others were of indifferent value and others were toxic. The effects of urea were generally beneficial according to these investigators.

When urea was subsequently manufactured synthetically and sold at a low price by German chemists it came to be extensively used as a source of nitrogen.

Denitrification:- The reduction of nitrates to free nitrogen or other forms through the activities of microbes was not correctly apprehended until the foundations of bacteriology had been laid. DAVY believed (1813) that free nitrogen might be liberated in the course of decomposition of organic matter, but he could not prove the assumption. Subsequently the evolution of nitrogen from sewage and from putrefying organic matter attracted the attention of ANGUS SMITH, a chemist, who published (1867) a memoir on the subject of the decomposition of nitrates in sewage. SCHÖNBEIN stated (1867) that soil nitrates were reduced to nitrites. Subsequently WARINGTON observed (1881) that soils could not only convert nitrate into nitrite, but could eventually destroy the latter. DEHÉRAIN and MAQUENNE reported (1882) that they found an appreciable reduction of nitrate in the absence of oxygen in field soils, especially at low temperatures. KELLNER's investigations in Japan (1884) showed that there were losses of over 90 percent of the nitrates from the soils of rice fields when flooded. However, he found that rice plants, especially when young, made better growth when the nitrogen was furnished as ammonium salts. From these and other observations it was obvious that the phenomenon was one of great importance for agriculture.

The role of bacteria in denitrification was suggested (1875) by MEUSEL, who observed the organisms, and by means of antiseptics inhibited the reduction of nitrates. Subsequently GAYON and DUPETIT, with more adequate bacteriological methods, isolated (1882) and made pure cultures of a number of nitrate reducing organisms.

The word "denitrification", used for the first time in 1882 by GAYON and DUPETIT, designated an actual denitrification, *i.e.*, a reduction of nitrate by bacteria with free nitrogen as the end point. The term is still applicable, although there has been a lack of consistency in its use.

It was at one time supposed that the losses in barnyard manure were due chiefly to the escape of ammonia, but later investigators believed that the losses are due to the escape of elemental nitrogen. Active discussion of the effects of denitrifying bacteria was stimulated by the opinion advanced (1895) by WAGNER, who thought that the addition of barnyard manure might lead to serious losses of nitrates from the soil, since it adds large numbers of denitrifying organisms. DEHÉRAIN and MARCILLE reported (1897) that manure applied in the ordinary amount causes no loss of nitrate. As a matter of fact, they could demonstrate an actual gain in nitrates. STUTZER and JENSEN reported (1897) that the activity of denitrifying bacteria is dependent on their access to a supply of organic material capable of yielding energy, if necessary utilizing rather resistant materials.

Eventually it was found that the activities and distribution of organisms which reduce nitrates are more extensive than at first suspected. HJ. JENSEN in 1898 and MAASSEN in 1901 reported that organisms of the colon group, as well as those of the putrefying group represented by *Pseudomonas pyocyaneus,* were active nitrate reducers. BAUER in 1901 showed that denitrifying organisms live

in the sea. Others have extended the knowledge of marine denitrifying bacteria. In contrast to the earlier conclusion of LAURENT that the reduction of nitrate to nitrite occurred only under anaerobic conditions, GRAN reported (1901) that certain marine bacteria actively reduced nitrates to ammonia when thoroughly aerated. GILTAY and ABERSON (1892) and MAASSEN (1904) concluded that the reduction of nitrate affords an important supply of energy for the organisms, rather than a nutrient.

Favorable conditions for the occurrence of a limited nitrate reduction in all soils are occasionally found. SCHLÖSING observed (1873) in oxygen-free soil a significant reduction of nitrate with a very small increase in ammonia. LIPMAN and BROWN determined (1908) that the decrease in nitrate in fertile soils could be referred provisionally to a reduction process. The precise importance of the reduction of nitrates, however, awaits further elucidation.

NIKLEWSKI concluded (1912) that nitrate reduction is a process of hydrogenation rather than one of denitrification in which there is an oxidation of hydrogen accompanied by a decomposition of NO_3. He found two organisms which exhibited marked ability to oxidize hydrogen and designated them *Hydrogenomonas flava* and *H. vitrea.* The system hydrogen-nitrate may be used as a source of energy according to NIKLEWSKI who thought that it is a special characteristic of the denitrifying organisms which utilize NO_3 as an oxidizing agent. Moreover, he was quite convinced that many organisms inhabiting the soil are capable of utilizing NO_3 for the oxidation of hydrogen in the absence of free oxygen.

The apparent confusion in the concepts of the denitrification process may be due to the fact that inadequate recognition has been given to the association of aerobic with anaerobic organisms. The aerobes may reduce the oxygen tension to a point where the anaerobes may simultaneously reduce the nitrates present to nitrites and ammonia.

The concepts and terminologies of the subject were considerably clarified (1904) by HJ. JENSEN's classification in LAFAR's Technical Mycology (vol. 3) in which he listed the phases of nitrate reduction as: (1) Reduction of NO_3 to NO_2 and NH_3; (2) Reduction of NO_3 and NO_2 to gaseous combinations of N and O; (3) Reduction of NO_3 and NO_2 with liberation of elementary N; (4) Transformation of nitrate N into organic compounds; (5) Liberation of elementary N by the decay of organic compounds.

The earlier reports on nitrate reduction by fungi were confirmed and extended (1889 and 1890) by LAURENT who demonstrated that species of *Alternaria, Cladosporium, Penicillium,* and other fungi carry on that process. KOSSOWICZ reported (1914) that the denitrifying action of mold fungi produced in some cases NO_2 and in others NH_3.

This brief survey of the work on nitrogen assimilation may indicate the results of a century of work on a phenomenon of great importance for plants. Scientific researches have elucidated many of the principles which determine the equilibrium between the nitrogenous components of atmosphere, soil, and plant. Out of them have come some rational ideas on the intricate processes by which the important protein constituents of the plant are evolved.

REFERENCES:-

BOUSSINGAULT, J. B. (1860): Agronomie, chimie agricole et physiologie. 2e édit., Mallet-Bachelier, Paris.
GREEN, J. R. (1909): A history of botany. Clarendon Press, Oxford (with bibliography).
LAWES, J. B., and GILBERT, J. H. (1888): On the present position of the question of the sources of the nitrogen of vegetation. Phil. Trans. Roy. Soc. 43:108-116.
LIEBIG, J. (1840): Die organische Chemie in ihrer Anwendung auf Agricultur und Physiologie. Vieweg, Braunschweig.
LÖHNIS, F. (1935): Handbuch der landwirtschaftlichen Bakteriologie. 2te Aufl., Borntraeger, Berlin (with bibliography).
RUSSELL, E. J. (1937): Soil conditions and plant growth. Seventh ed., Longmans, Green, London and New York.
SHENSTONE, W. A. (1901): JUSTUS VON LIEBIG, his life and work (1803-1873). Cassell. London.

Chapter XV.

THE FIXATION AND METABOLISM OF NITROGEN.

The importance of nitrogen in the life of the organism and the ways in which it functions were problems not easily solved for many years after the pioneer researches mentioned in the preceding chapter. The phenomena could not be adequately explained until developments in the sciences of chemistry and bacteriology revealed agencies which were comprehended so vaguely by the early workers. The discovery that nitrogen enters the organic world from the vast atmospheric ocean through such a narrow portal was one of the great accomplishments of science in the last half-century. Until the recent development of electro-chemical industries the world's supply of nitrogenous compounds came principally from the vital processes of plant cells.

Some of the salient scientific discoveries by investigators of the biological aspects of nitrogen accumulation will be found in this brief chapter. At the present moment it is impossible to estimate the importance of the process of nitrogen fixation in biological evolution, or how it has affected racial developments, migrations of the human race, and kindred phenomena. An adequate discussion of this fundamental factor awaits the attention of some biological historian.

Nitrogen fixation by non-symbiotic organisms:- BERTHELOT stated (1892) his belief that microörganisms may enrich the nitrogen content of soil on which no seed-plants grow and from which all other supplies of nitrogen (except atmospheric nitrogen) are excluded. He observed that the process stopped in winter and was, at any time, completely inhibited by heating the soil to 100°C. DEHÉRAIN and others confirmed these observations. Although unsuccessful in isolating the actual organism which effected the nitrogen-fixation, BERTHELOT ascribed the function to a series of organisms in field soils. The absence of exact information about the effective agent sent investigators on divergent tracks for a number of years. SCHLÖSING and LAURENT, who cultivated numerous plants in the absence of nitrogen compounds, found (1891) that in certain cases a small amount of nitrogen was fixed, but that a suppression of the algal growth put an end to nitrogen-fixation.

In the midst of the discussions and criticisms of the concept of bacterial fixation, WINOGRADSKY announced (1893) his discovery of *Clostridium Pasteurianum* in soils. This large anaerobic organism, which resembles *Clostridium butyricum*, was able to obtain its nitrogen from air which had been carefully purified from ammonia and other compounds, and, when grown in sugar-containing solutions, it produced butyric and acetic acids, thereby obtaining a source of energy. From cultures on artificial media containing 4 percent sugar the gain in combined nitrogen in a few weeks amounted to approximately 2-3 mg. per gram of sugar utilized.

WINOGRADSKY made the important observation that in nature *Cl. Pasteurianum* nearly always occurs in association with two other bacteria, from which it can be separated only with difficulty, since all can develop in a medium low in fixed nitrogen. When isolated it is an obligate anaerobe, but when in association with these other bacteria, it can grow under apparent aerobic conditions and fix nitrogen, since they appropriate the oxygen for their own metabolism. The anaerobic organism can live in the aerated part of the soil if it is associated with those oxygen absorbing bacteria, or with certain fungi, yet not every organism can play a protecting role, only those which begin actively to utilize oxygen, and at the start they must have a supply of combined nitrogen afforded them. WINOGRADSKY found that nitrogen-fixation proceeded more rapidly in mixed cultures if a small amount of ammonia or nitrate was first added.

WINOGRADSKY tested a large number of organisms with respect to their nitrogen-fixing ability, but found only two which had even a weak ability to fix nitrogen. Later it was found that some other butyric acid bacteria may fix appreciable amounts of nitrogen.

It was 1901 when the problem bequeathed by BERTHELOT was solved by BEIJERINCK, who isolated from soil and described a large aerobic organism for which he created the genius *Azotobacter*.

When BEIJERINCK introduced soil as an inoculum into solution cultures which contained glucose as the carbon supply but lacked fixed nitrogen compounds he obtained *Cl. Pasteurianum* along with *Azotobacter* and other forms. If he supplied carbon in the form of mannite or potassium or sodium proprionate, the cultures supported a growth of *Azotobacter* relatively free from other organisms. KOCH reported (1911), and others have corroborated the report, that *Azotobacter* fixes more nitrogen per unit weight of sugar decomposed than *Cl. Pasteurianum*. For example, from 1 g. of sugar *Azotobacter* could obtain energy for fixing 15 mg. nitrogen, while the *Clostridium* could fix only 2-3 mg. with the same amount of sugar. BEIJERINCK described two species, *A. chroococcum* and *A. agile;* the first was obtained from garden soil, the second from canal water at Delft. The first is a large, round to rod shaped cell which forms membranes on the surface of liquid media, which tend to become brown or black with age, and oxidizes carbon compounds to carbon dioxide and water. The second is a motile, large, transparent cell with a green fluorescence. KENTNER, LIPMAN, FISCHER and others have demonstrated that *Azotobacter* is widely distributed on land and in fresh water bodies.

The effects of nutrient conditions upon the physiology of *Azotobacter* were extensively studied with respect to mineral constituents and organic constituents. PRAZMOWSKI demonstrated (1912) the importance of iron, especially the hydroxide, $Fe(OH)_3$, and BORTELS (1930) the essentiality of molybdenum for *Azotobacter*. This organism has such a definite requirement for phosphates that it was used by CHRISTENSEN (1923) for classifying soils with respect to their phosphate content.

LIPMAN in New Jersey and GREIG-SMITH in Australia reported (1906) that the fixation of nitrogen by *Azotobacter* was enhanced by several associated bacteria. FISCHER and others, as will be noted subsequently, have speculated on the beneficial effects of algae on *Azotobacter*, finding it easier to demonstrate an increase

in nitrogen-fixation in artificial cultures than in field soil. PRINGSHEIM reported (1911) that other species of bacteria were capable of fixing free nitrogen, but they seemed to have less efficiency per unit of sugar than *Azotobacter.* PURIEWITSCH reported (1895) that the fungi, *Aspergillus niger* and *Penicillium glaucum,* when grown on a medium containing inorganic salts, tartaric acid, cane sugar, and ammonium nitrate, fixed small amounts of nitrogen. A few other workers obtained confirmatory results, but the majority have obtained negative evidence. The discoveries concerning the algae will be summarized on a later page of this chapter.

Nitrogen fixation by symbiotic organisms:- The outlines of the successful work on the phenomenon of nitrogen fixation by symbiotic bacteria are so well known that a brief recital of the historical developments will suffice.

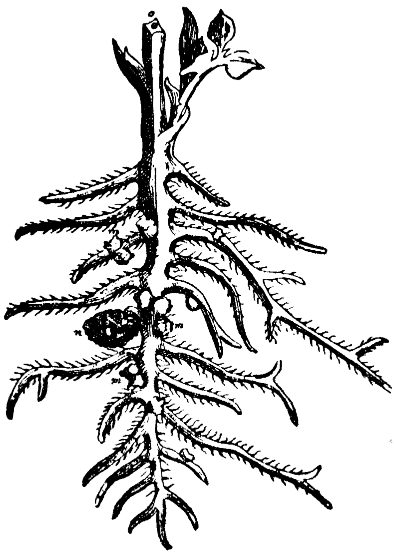


FIG. 25. — MALPIGHI's figure of a *Vicia Faba* root, bearing nodules (m. m), from Opera Omnia, Vol. 1, 1687 (Leyden).

MALPIGHI observed the galls on legume roots and published an accurate figure of a *Vicia Faba* root bearing nodules in "Anatome Plantarum" in 1679 and reproduced it in "Opera omnia" in 1687. He made the trenchant statement that the nodules were not caused by insects, but he could go no further with the means of investigation at his command. BOUSSINGAULT, whose work has already been mentioned, reported (1838) that peas and clover could get nitrogen from the atmosphere, whereas wheat could not. Fortunately for science the problem was eventually attacked by men whose efforts were crowned with success.

In the latter part of the 19th century various workers in Germany, France, England, and the United States again attacked the question, utilizing field and pot experiments. Working independently they obtained new and stronger evidence that leguminous plants acquire nitrogen from the atmosphere. ATWATER of Connecticut demonstrated (1883 and 1885) that the nitrogen acquired

by peas was 50 percent of the total quantity harvested and he believed that this gain was due to their power to utilize free atmospheric nitrogen.

It remained for the Russian botanist, WORONIN, to demonstrate in 1866 that the nodules of legume roots are replete with bacteria but the nature of the nodules remained a subject of lively controversy for some time thereafter. H. MARSHALL WARD made a careful study of the plants and their nodules, demonstrating that the formation of root nodules was dependent upon an infection. For example, *Vicia Faba* plants when grown in sterilized solutions produced no nodules, but readily produced them if pieces of chopped nodules were placed in contact with their root hairs. He saw and described the characteristic infection strands which penetrated the root hairs and passed into the cortical cells.

The protracted investigations of the relation of plants to the acquisition of nitrogen begun by DE SAUSSURE, VILLE, LAWES and GILBERT and others culminated in the discovery of symbiotic fixation by HELLRIEGEL and WILFARTH in 1887. The last named workers grew plants in calcined soil as others had done, but to some of the pots they added leachings from a fertile soil, in other words, an inoculum containing bacteria of the proper species and variety. They found that peas growing in the inoculated soils produced root nodules, and, after an initial period of nitrogen deficiency, turned green and made thrifty growth. On the contrary, peas in similar soil without an inoculum were unthrifty and perished prematurely. They were most emphatic in their statements that the legumes are unable to assimilate free atmospheric nitrogen unless they have the active participation of microörganisms with which they enter into a symbiotic relationship. They further stated that graminaceous plants stand in a different category with respect to their nitrogen nutrition, being entirely dependent upon a supply of fixed nitrogen in the soil. GILBERT of Rothamsted was present at the meeting in Berlin at which HELLRIEGEL gave the preliminary statement of his results in 1886. Returning to Rothamsted, he confirmed HELLRIEGEL's discoveries and later published his findings in collaboration with LAWES. It then became evident that the failure of the early experiments had been due to conditions which precluded the entrance or development of the bacteria. These discoveries of the unique symbiotic fixation of nitrogen which attracted widespread attention in the realms of agriculture and science have been tremendously expanded by many workers. The work has been many times repeated and commented upon so that a vast literature upon the subject has been produced, thus a greater appreciation of the nitrogen cycle in nature has been obtained.

There were originally many divergent views of the nature of the nodules and of the associated organisms. BRUNCHORST coined (1885) the term "bacteroid" (bacteria-like) to designate the tiny bodies in the nodule, regarding them, not as living organisms, but as "organized protein bodies". In spite of BRUNCHORST's misapprehensions, the term bacteroid has been adopted by most bacteriologists who have studied them.

TSCHIRCH maintained (1887) that bacteroids were not living organisms since he was unable to cultivate them in any of the media he employed. It is probable that he and others arrived at erroneous conclusions because they were looking for branched

rods in the cultures and failed to recognize the unbranched rods as legume bacteria. The problem was solved by BEIJERINCK who demonstrated (1888) that the bacteria-like bodies in the nodules are true bacteria and named them *Bacillus radicicola.* PRAZMOWSKI simultaneously adduced evidence confirming BEIJERINCK's conclusions, showing that legume roots could be artificially infected with organisms from the laboratory cultures with a resultant production of nodules.

Within a few years after the identification of the nodule bacteria it was discovered that certain strains had a specificity previously unsuspected. HELLRIEGEL found that bacteria from clovers could not produce nodules on lupines and serradella. NOBBE and HILTNER found (1898) similar relationships with other legumes and formulated the concept that each legume had its particular species of nodule-forming bacteria. The observed specialization according to their idea was the result of continued association through which the bacteria were modified to an extent which rendered them unable to invade the roots of other legumes. The species relationship of the nodule-formers was not at first correctly apprehended and for a long time it was not scientifically studied. The name *Bacillus radicicola* given (1888) by BEIJERINCK who first obtained it in pure culture was not retained. The specific name *Rhizobium leguminosarum* which had been coined (1890) by FRANK was subsequently applied by WINSLOW, though it was apparent that organisms from different hosts were not identical. BALDWIN and FRED, upon the basis of host relationships, morphology and cultural characters, proposed (1929) six species of nodule-forming, nitrogen-fixing organisms, namely:

SPECIES	HOST PLANTS
Rhizobium leguminosarum, Frank	*Lathyrus, Pisum, Vicia,* and *Lens.*
Rhizobium trifolii, Dangeard	*Trifolium.*
Rhizobium phaseoli Dangeard	*Phaseolus vulgaris, Ph. angustifolia* and *Ph. multiflorus*
Rhizobium meliloti Dangeard	*Melilotus, Medicago,* and *Trigonella.*
Rhizobium japonicum (Kirchner) Baldw. and Fred	*Soja Max.*
Rhizobium lupini (Schroeter) Baldw. and Fred	*Lupinus.*

The manifold relationships between the bacteria and their host plants have been studied extensively, in many laboratories. Many new strains have been discovered and the symbiotic relations have been somewhat elucidated, yet the exact mechanism of nitrogen fixation and the part played by each of the symbionts is not known. FRANK believed (1889 and 1890) that nitrogen is assimilated through the leaves and that the associated bacteria merely accelerated a process occurring in a non-nodulated leguminous plant. KOSSOWITSCH (1892) and WHITING (1915) demonstrated by rigorous gasometric measurements that a nodulated legume actually absorbs nitrogen through the roots. THORNTON has extended (1930) the work of others and shown that nitrogen fixation and carbohydrate synthesis are closely correlated. The fixation of nitrogen by *Rhizobium* in the absence of the host plant was originally taken for granted and several investigators reported positive results, but subsequently workers with refined techniques have been unsuccessful in demonstrating fixation by the organism in pure

cultures on laboratory media. WILSON reviewed (1937) the work and discussed the validity of the results of various workers. VERNER and KOVALEV have reported (1936) that *Rhizobium* could independently fix nitrogen if furnished with "Bios" from a suitable source. The suggestion awaits verification by other observers.

VIRTANEN advanced (1933) the idea that hydroxylamin is the first product in the process of nitrogen fixation. He demonstrated that the benefit to an associated non-legume came from nitrogen transferred to it from the legume, and found that soluble nitrogen compounds accumulate in the substrate if no non-legume is present. The process of amino acid formation by legume bacteria may be briefly described as follows: Hydroxylamine and oxalacetic acid react to form an oxime, in this case, oximinosuccinic acid, which contains a chain of four carbon atoms. The next step in the process is the formation of l-aspartic acid, which, by decarboxylation, is converted into β-alanine. In younger cultures the nitrogen is largely composed of l-aspartic acid, in older cultures, β-alanine. VIRTANEN and LAINE postulated the steps by which an amino acid is produced by nitrogen fixing organisms from carbohydrate and free nitrogen as follows:

N_2 → hydroxylamine ——→ ↘
oxime of oxalacetic acid → l-aspartic acid.
carbohydrate → oxalacetic acid ↗

They showed that in the presence of crushed pea plants aspartic acid can donate amino nitrogen to pyruvic acid with the formation of alanine. In all, except the earlier stages, the process of protein synthesis from free nitrogen does not, therefore, differ from that by which proteins are formed from ammonia nitrogen.

Soil inoculation:- Within a very short time after the discovery of HELLRIEGEL and WILFARTH was announced, interest arose in the question of introducing the necessary bacteria into field soils, to promote the development of nodules. It was logical to assume that if these bacteria are so important, one should be sure that he had in the soil a small number of the desired organisms. Moreover, it was thought that the presence or absence of the organisms might explain the reasons why clover and other legumes failed to thrive in certain soils. If these nodule bacteria enabled the plant to lay hold and avail itself of the atmospheric nitrogen, it was hoped that the farmers would be relieved of the cost of buying outside sources of nitrogen for their soils. At the outset, the inoculation was carried out by the transfer of soil from a field in which the legumes had grown, and which presumably contained the necessary organisms. Later on, for various reasons, the attempt was made to cultivate the organisms on artificial media and distribute them to farmers to apply to the soil or the seed of the crops which they desired to plant. SALFELD published a work in 1896 in which he recounted his experiments on soil inoculations and claimed that they were, on the whole, very beneficial to the crops which were to be grown. It should be noted, however, that in many cases the inoculations were restricted to reclaimed moor soils of northern Europe. In the last years of the nineteenth century, many studies were made of the possibilities of soil inoculation. Some were suc-

cessful, others were failures. Gradually attention was directed to the possibility of the artificial culture method. NOBBE and HILTNER put on the market a preparation which was sold under the trade name of Nitragin on which they obtained patents in various countries. The results from the commercial culture were quite variable. In some places increased yields were obtained, and in other cases no result whatever was observed.

In the United States, work was undertaken by the Federal Department of Agriculture and by certain state experiment stations, which undertook to cultivate the organisms on a medium low in combined nitrogen, and to distribute these cultures as cheaply as possible for the benefit of the farmers. Some cultures were absorbed on cotton and distributed in tin boxes; others were made in liquids and sent out in bottles. In certain cases where plants were being grown in new regions for the first time, the effects of inoculation were decidedly beneficial, but in many other cases the farmers were sadly disappointed in the results of inoculation. Extravagant claims were generally made by the manufacturers of commercial cultures as to the benefits to be derived from their use. In the end, the faith of the farmers in the efficacy of artificial cultures was greatly weakened. Eventually it was discovered that it was of more importance to put the field soil into proper condition than it was to inoculate it with bacteria. The failure of legumes was frequently traced to lack of aeration or to high acidity of the soil or to lack of organic matter which impaired the water-holding capacity of the soil.

The subject of inoculation was actively investigated for many years without, however, arriving at concordant results. HILTNER and others assumed that the variable results might be due to unequal virulence of the nodule-forming bacteria. WILSON considered (1937) that cross-inoculation of legumes and nodule bacteria is somewhat indefinite owing to strain variation among the bacteria, and to host specificity in the plants observed. Certain strains of the soy bean organism are able to invade only one or two members of the cowpea group, whereas others will infect nearly all the members that have been tested. Conversely, certain plants appear to be immune to organisms except those isolated from the same genus or species; others are readily invaded by organisms isolated from different genera.

The effects of bacteriophage on the nodule-forming bacteria, suggested (1932) by LAIRD, have not as yet been definitely shown to be a factor in infection. It is true that the phage seems to be widely distributed and that races isolated from nodules are known to cause lysis of a given culture of the nodule organisms. DEMOLON and DUNEZ held (1935) that bacteriophage might be responsible for the "fatigue" of alfalfa soils in France and ascribed the failure of alfalfa to that factor. They reported that since the phage was sensitive to dessication, sunlight, temperatures below 10°C., etc., the phage would in time disappear from the soil. VANDECAVEYE and KATZNELSON adduced (1936) similar evidence from experiments on soils in the Yakima district in the state of Washington, showing that a lytic principle could be isolated from soils in which alfalfa had been grown for three years. They found that the formation of nodules was poorer on fields from whose soils lytic principles were obtained.

Non-symbiotic nitrogen-fixation by green plants:- The theory that all living plant cells have the power to assimilate gaseous nitrogen has come into prominence from time to time in one form or another. A complete negation of the theory has not yet been afforded. As a matter of fact it is embarrassingly difficult to explain why one cell more than another should possess that unique power. This was at the heart of the problem which engaged BOUSSINGAULT, VILLE, and LAWES a century ago. Following the discoveries of nitrogen-fixing bacteria in the latter part of the nineteenth century the theory fell into abeyance, but came to the fore again in the early part of the present century. It is one of those biological problems which advances and retreats, but never disappears. FRANK seems to have been the first to raise the question of assimilation of free nitrogen by all plants, regardless of symbiotic organisms. He did not employ a sterilized soil and admittedly found algae in it. PETERMANN conducted better experiments and found (1892) that barley was unable to fix nitrogen in a sterilized soil, although he had reported in earlier researches that plants grown in a soil containing algae and bacteria displayed an energetic fixation of nitrogen. SCHLÖSING and LAURENT showed (1892) that the apparent fixation of nitrogen by oats, mustard, and cress was completely abrogated by suppressing the growth of algae in the soil.

When MAMELI and POLLACCI announced (1911) that certain plants showed an increase in nitrogen when grown in nutrient solutions containing a small amount of combined nitrogen in addition to the usual mineral salts there was a revived interest in the phenomenon. The technique used by the authors was much more refined than that employed by the workers in the first half of the nineteenth century and was calculated to inspire confidence in the results. Their failures, as well as successes, were reported. They concluded that the process of nitrogen-fixation is rather widely distributed among green plants and formulated the hypothesis of a catalyser in the living substance capable of nitrogen-fixation resulting in the production of ammonia. LIPMAN and TAYLOR, who attempted to refine the technique of growing flowering plants, reported (1924) that they obtained a significant increase in nitrogen in wheat and barley but not in peas.

The possibility that certain algae might function as fixing agents for nitrogen was strongly suggested in 1889 by FRANK's results with mixed cultures in which *Oscillaria, Ulothrix, Pleurococcus,* and *Nostoc* were present. Three years later SCHLÖSING and LAURENT found in their mixed cultures (in which *Nostoc* was present) a significant gain in fixed nitrogen. The results of other workers were variable due in part to the inevitability of using mixed cultures and to faulty technique. SCHLÖSING and LAURENT found that the absence of *Nostoc* from mixed algal cultures resulted in lack of nitrogen fixation. BEIJERINCK's cultures demonstrated (1901 and later) that cultures of blue-green algae especially *Anabaena* and *Nostoc* will grow and fix significant amounts of nitrogen on solutions containing little combined nitrogen. SCHRAMM who subsequently investigated (1914) the question found no ability to fix nitrogen in the *Chlorophyceae.* In the controversial era which followed MOORE and WEBSTER reported (1920 and 1921) that algae could fix free nitrogen but admitted

that it was quite possible that bacteria were present in the cultures, although they noticed no turbidity after 8 days. WANN concurred (1921) in the reports that certain algae could fix appreciable quantities of atmospheric nitrogen in the presence of nitrate. His experiments were conducted with pure cultures of algae and contained glucose as well as nitrate. BRISTOL and PAGE severely criticised (1923) the chemical methods which WANN employed for the analysis of his cultures, condemning the entire work. They concluded their publication with:

"The chemical methods used by the present authors were free from the serious sources of error in those used by WANN. While it is quite conceivable that green algae might assimilate atmospheric nitrogen under certain conditions as yet unknown, there is so far no trustworthy evidence that they can do so".

The majority of microbiologists came to the conclusion that the power of nitrogen fixation among the algae is restricted to *Nostoc* and *Anabaena* in the *Cyanophyceae,* though FISCHER propounded (1916) and PRINGSHEIM agreed (1918) that the results were due chiefly to the beneficial association of algae and nitrogen-fixing bacteria.

Nitrogen metabolism:- The nature of the nitrogen compounds in plants is admittedly complex and it is small wonder that a subject so profound has taxed the powers of many modern investigators. A few men of vision made observations based on simple experiments in the latter part of the 18th century, but the original advances were not actively prosecuted until later.

ROUELLE separated (1773) a glutinous substance from the sap of plants and recognized that it was like the gluten of wheat. After coagulating the substance by the use of moderate heat he separated it and found that it gave rise to the same products as wheat gluten and that it could be changed into a body having an odor like cheese. Many a year passed before anyone improved upon the method of fractional heat coagulation used by ROUELLE.

The changes in the organic nitrogen accompanying germination and growth were studied (1806) by VAUQUELIN and ROBIQUET who obtained asparagin from asparagus shoots and demonstrated that it contained nitrogen. It remained for PIRIA to demonstrate (1844) that asparagin may be formed during the germination of plants other than asparagus. He examined vetch seedlings which had germinated in the dark and from them prepared a small quantity of asparagin. Being unable to find any asparagin in ungerminated seeds, PIRIA concluded that it was something arising from a change in a nitrogenous reserve substance during germination, a conclusion which was perfectly correct and which anticipated in many ways investigations carried on fifty years later.

The significance of organic nitrogenous substances in the metabolism of the plant was clearly envisioned by BOUSSINGAULT and summarized in 1868. He showed that the asparagin produced in seedlings in darkness can again be utilized by the plants under the action of light. BOUSSINGAULT surmised that the asparagin formed might be part of the respiratory mechanism of the plant itself, although it was not proved by chemical analysis until several years later that the asparagin observed was derived from proteins. PFEFFER adduced (1872) evidence that the total nitro-

gen in the germinating seed remains constant, unless some form of soluble nitrogen is added to the medium in which the plant is growing. The nitrogen in the seeds of leguminous plants, he observed, is practically all protein nitrogen. When asparagin appeared, he regarded it as a primary product of protein metabolism and assumed that the asparagin formed in the cotyledons might diffuse out into the axial organs where, if carbon and hydrogen were present from some source such as carbohydrates, it might be regenerated to form protein, although the composition of the newly formed proteins might differ from that in the cotyledons; in the absence of available carbon and hydrogen, asparagin would accumulate in the seedlings. PFEFFER's work was hampered by the lack of knowledge of other nitrogenous constituents derived from proteins. In 1872 the only constituents which were well known besides asparagin were ammonia and nitric acid. Knowing that ammonia was toxic and that nitric acid as such did not occur in plants, he came back to the opinion that asparagin was the form in which most of the nitrogenous substances were transported from cell to cell. He limited his study to leguminous plants, knowing that there were whole families of plants in which it was impossible at that time to demonstrate the presence of asparagin. He concluded that the problem of transportation was probably of importance only in the early stages of growth, assuming that the developing plant was probably able to meet its needs by assimilating the salts of ammonia or nitric acid drawn from the soil. Although PFEFFER oversimplified the problem he opened a new field for research.

SCHULZE made great advances in the knowledge of protein metabolism and reduced the subject, so far as possible, to a quantitative basis. His first paper described (1876) the changes in composition of seeds of yellow lupine during germination and up to the twelfth day of age of the seedlings, at which time they contained over 18 percent of asparagin on the dry-weight basis. Yet even that relatively large percent did not account for the loss of all the protein nitrogen, so he assumed that "amino-nitrogen" had been formed. As a matter of fact about one-fifth of the vanished protein nitrogen could be recovered in the form of amino nitrogen. While there had been a loss of "dextrinous" material, there had been a fluctuating gain in glucose. Whatever uncertainty we may feel at the present time in interpreting this work, we can see that he had shown that the lost proteins had been transformed during germination and seedling growth partly into asparagin and partly into other products, including amides. This conclusion obviously differed from that of PFEFFER, who assumed that protein disintegration gave rise directly to sugars and to asparagin, and that protein regeneration in the new parts of plants consisted entirely in the recombination of these two substances.

A period of active study and discussion followed. Not all of the findings could be harmonized at the time they were made. Particularly baffling was the fact that many plants contained large amounts of asparagin and others none. To make the matter more puzzling, IVAN BORODIN found (1878) that leaves cut from the shoots of trees might contain no asparagin, but if placed with the cut ends in water in darkness, they would subsequently contain

appreciable amounts of asparagin. Whence came this asparagin? BORODIN concluded that in living plant organs, it is probable that protoplasmic activities such as respiration require a continuous breakdown and regeneration of proteins. This process of breakdown would give rise to asparagin. If sufficient carbohydrate were available in the form of sugar, the asparagin would be regenerated to protein, if not, it would accumulate in the plant. PFEFFER opposed the conclusions of BORODIN, but SCHULZE accepted them, stating that they helped to explain many of his observations, and later obtained evidence to support BORODIN's theory. SCHULZE suggested that plants in which asparagin could not be found might contain the acid amide, "glutamine". In that case the failure to find asparagin in plants of the cruciferae might be due to the fact that they contained glutamine instead of asparagin. VIRTANEN and LAINE suggest that, if aspartic acid should be the only primary amino acid formed during nitrogen fixation, then the synthesis of other amino acids must take place at its expense. They supported (1936) this suggestion by the demonstration that, in the presence of crushed pea plants, alanine could be formed from asparagin and pyruvic acid.

PFEFFER concluded that light is not essential for the synthesis of proteins since the process may proceed in fungi in the absence of light and chlorophyll. In the seed plants it is evident that there is a certain amount of specialization in the assimilation of nitrogen which PFEFFER thought culminated in leaves and other chlorophylliferous organs. The roots, however, seem also able to assimilate nitrates and often to form proteins from the amides which are conveyed to them. It was possible, he thought, that all cells in a plant might be capable of assimilating relatively simple nitrogen compounds. FRANK and OTTO found (1890) that leaves of *Trifolium* contained more asparagin in the evening than on the following morning and that leaves of *Trifolium, Medicago,* and *Lupinus* likewise contained more total nitrogen in the evening than on the following morning. They concluded from these observations that the first stages in the synthesis of nitrogen compounds were accelerated by light.

STOKLASA concluded (1916) from experiments with sugar beet seedlings that protein synthesis is not strictly limited by light. He thought that it can proceed in darkness if carbohydrate and nitrate, or ammonia, and all essential mineral salts are present; however, light benefits these reactions by affording a supply of energy. He suggested that in the darkened plant potassium is able to accelerate the breakdown of carbohydrate by respiratory enzymes. In view of the unsatisfactory nature of much of the evidence presented by STOKLASA and others it is not yet possible to decide whether light has any direct influence on the synthesis of protein or its precursors.

In the vast array of researches which started about that time on the changes in protein during metabolism in the plant, SCHULZE clearly maintained the lead. His chief opponent was PFEFFER. Eventually SCHULZE arrived at the conclusion that the amino acids and other products resulting from the decomposition of the reserve proteins in the cotyledons were transported to the axial organs of the plant before conversion into asparagin, and that this was what had induced him to suggest first his old, and later his new, hypothe-

sis of asparagin formation. The new mechanism of asparagin synthesis, however, led him to adopt the opposite view and to regard asparagin or glutamine as more easily available for protein synthesis than the amino acids. Asparagin formation was thus the first phase of protein regeneration. PRIANISCHNIKOV, however, opposed this idea and criticized (1899) much of the evidence brought forward by SCHULZE. He disputed the idea that asparagin and carbohydrates could be said to bring about the regeneration of proteins, stating that there was no evidence of the utilization of asparagin in etiolated seedlings, even when carbohydrates were supplied. He pointed out that asparagin formation is known to be most rapid in the early periods of germination while seeds still contain adequate carbohydrate supplies. He concluded that protein is regenerated from amino acids, rather than from asparagin, as the concentration of the latter is shown to have increased.

The nature of proteins in seeds was greatly elucidated in the opening years of the 20th century by T. B. OSBORNE, who developed methods for their isolation and purification, by means of which he discovered the chemical differences in proteins of various plants. His work revealed an imposing number of vegetable proteins. OSBORNE considered that the amino acids are for the most part united in the protein molecule in polypeptide union; that is, by the union of the NH_2 group of one amino acid with the carboxyl group of another.

ZALESKI and SHATKIN reported (1913) results which seemed to support the conclusion stated by PRIANISCHNIKOV—namely, that protein is regenerated from amino acids. They observed an increase in protein nitrogen in bulbs of *Allium Cepa* growing over water accompanied by a decrease in the concentration of amino nitrogen, but not of amide nitrogen. Originally, PRIANISCHNIKOV seemed to consider that asparagin was a harmless means for the storage of ammonia, a substance which in itself would be injurious to the plant. From a long series of investigations he eventually adduced new evidence on the transformations of nitrogen in the plant. Out of it came the far-reaching concept that amide formation in the plant requires, not protein, as had been formerly supposed, but only ammonia and some non-nitrogenous precursor such as glucose, or perhaps some other nitrogen-free material. This concept opened a new chapter in the study of nitrogen assimilation by plants and is now widely accepted. MASON and MASKELL support PRIANISCHNIKOV's ideas on protein formation, showing that the concentration gradients in the cotton plant suggest that it is the amino and residual nitrogen which is transported from the leaves to the boll, and that the concentration of amides in the stems is due to the storage of these materials. The work reported (1930) by BISHOP also showed that during the development of the barley grain, the non-protein nitrogen, which is obviously the form in which it is translocated from the leaves, never exceeds a certain maximum concentration; and as more and more nitrogen enters the grain during development, it is forthwith used for the synthesis of the three constituent proteins.

Out of the mass of interesting and important researches, which, however, cannot be summarized in this place, we may look for the recent concept by which amino acids are produced by the living

plant. CHIBNALL outlined (1939) a chain of reactions, starting with an α-amino acid, going next to oxalacetic acid or some substance containing a chain of four carbon atoms. The ammonia assimilated by the root system may be condensed with the oxalacetic acid or with α-ketoglutaric acid, or both of these substances to produce aspartic acid, glutamic acid, or both amino acids. Either of these substances can then donate amino nitrogen to such α-ketonic acids as are available in the system and are required for amino acids, and hence for protein synthesis. When nitrogen is available in the form of nitrates, the synthesis of amino acids appears to depend primarily upon the process of reduction, although it is not clear just how all stages may transpire. It seems, however, that in the plant nitrate is reduced to nitrite; which goes to hyponitrous acid, and that in turn to hydroxylamine, which then goes to ammonia.

Investigations in the modern method were not undertaken on the problem of the synthesis and hydrolysis of leaf proteins until a comparatively recent date. CHIBNALL found that there was an apparent constancy in composition of protein preparations made from the leaves of the runner bean at intervals throughout the life history of the plant. From this he concluded that preparations of proteins of any reasonable degree of purity might be obtained without resort to treatment which brought about partial hydrolysis. A little later he devised the method of using ether or chloroform for removal of the contents of the cell vacuole and freeing the plant material from a large amount of mineral matter in solution. By this means, proteins were obtained in moderately good yields from the leaves of several plants.

By means of his new method, CHIBNALL was able to show that detached leaves of the runner bean suffered a marked breakdown of protein, with a simultaneous production of amino acid nitrogen, as well as of acid amides, when detached leaves were floated on water for five days. In 1926 MOTHES reported that the primary decomposition products in detached leaves of *Vicia Faba* were amino acids, which underwent subsequent transformation to give ammonia; hence asparagin or glutamine was postulated, and MOTHES concluded that this might be due to the lack of sufficient carbohydrates to provide the necessary energy for living processes, so that amino acid residues were being utilized in respiration. He found that detached leaves which are not too old, when exposed to daylight or fed with glucose in the dark, show no formation of amides. Those present disappear and are used for protein synthesis. He thinks that amides and ammonia arise directly from proteins or their decomposition products. His final conclusions on his experiments were somewhat as follows:

> The significance of amides cannot be primarily that of a medium of translocation. There is translocation of amides only if they, through accumulation, disturb the equilibrium in the region of their formation or if they are needed in young leaves for protein synthesis. In both the above cases, there is no ground for regarding them as other than substances in the form in which ammonia is rendered innocuous.

The large number and the complexity of the proteins constitute a serious problem for one who would attempt to give a brief clarifying view of their origins. ONSLOW concluded (1931) that protein may be synthesized in the meristematic tissues of growing

points and other regions, by the formation of a pattern, the result of condensation of small active molecules formed in glycolysis, nitrogen being supplied as ammonia, and sugar as sucrose. In leaves and other organs proteins may also be synthesized and hydrolyzed. The predominating effect, according to ONSLOW, depends both on the age of the organ and on the amount of carbohydrate present. Synthesis predominates in the youngest members, hydrolysis in the oldest. Abundance of carbohydrate is unfavorable to protein synthesis. With continuous fall in carbohydrate, hydrolysis proceeds to amino acids followed by deamination to amides (or ammonium salts of organic acids) and ammonia. At the growing points sucrose, the sugar of translocation, may be rapidly hydrolyzed, the gamma fructose being used in respiration, the inactive glucose in cell wall formation. As a result of the lack of carbohydrate at the growing point, amino acids would be converted into amides (or ammonium salts of organic acids), and these further yield ammonia.

The discussions of the diverse and, at times, discordant ideas of the acquisition and utilization of nitrogen have filled this chapter. Within a hundred years the subject has developed from numerous fragmentary opinions to a point where it has commanded the attention of specialists and men of genius. The biological importance of the nitrogen problem is increasingly recognized in many fields of science and new techniques are continually being applied to its investigation.

One of the scientific achievements of the last hundred years was the discovery of the process of nitrogen fixation and the salient steps in the nitrogen cycle in nature. The cultivation of leguminous plants which may supplement the activities of the non-symbiotic bacteria of the soil has become a means for regulating the nitrogen content of agricultural soils. Important results have, and will continue to flow from the study of the biochemistry of the nitrogen of plants.

REFERENCES:-

CHIBNALL, A. C. (1939): Protein metabolism in the plant. Yale Univ. Press, New Haven (with bibliography).

FRED, E. B., BALDWIN, I. L., and McCOY, E. (1932): Root nodule bacteria and leguminous plants. Univ. Wisconsin Studies in Science 5, Madison (with bibliography).

GREEN, J. R. (1909): A history of botany, 1860-1900. Clarendon Press, Oxford (with bibliography).

LAWES, J. B., GILBERT, J. H., and PUGH, E. (1861): On the sources of the nitrogen of vegetation, with especial reference to the question whether plants assimilate free or uncombined nitrogen. Royal Soc. London, Trans. 151:431-577.

LÖHNIS, F. (1935): Handbuch der landwirtschaftlichen Bakteriologie. 2te Aufl., Borntraeger, Berlin (with bibliography).

NIGHTINGALE, G. T. (1937): The nitrogen nutrition of green plants. Bot. Rev. 3:87-174 (with bibliography).

ONSLOW, MURIEL W. (1931): The principles of plant biochemistry. Cambridge Univ. Press, London.

OSBORNE, T. B. (1909): The vegetable proteins. Longmans, Green, London and New York.

RUSSELL, E. J. (1937): Soil conditions and plant growth. Seventh ed., Longmans, Green, London and New York.

VICKERY, H. B. (1938): The metabolism of proteins in green leaves. Cold Spring Harbor Symposia on Quant. Biol. 6:67-77.

VIRTANEN, A. I. and LAINE, T. (1939): The mechanism of nitrogen fixation. Biochem. Jour. 33:412-427.

Chapter XVI.

PLANT NUTRITION.

The plant physiologist of today, busy as he is with laboratory apparatus and concerned with the biophysical and biochemical aspects of the plant, finds it hard to realize the position of plant nutrition at the beginning of the nineteenth century, when laboratories and apparatus were virtually non-existent. There was another factor which retarded the development of plant physiology at that time. It was the dominance of the idea of vitalism, which had been inherited from the past, compounded with the often mystical language of the nature philosopher. The vitalists had a tendency to regard all nature as too mysterious and too esoteric to be capable of investigation. The nature philosopher, making a few radical premises, assumed that he understood the whole thing and proceeded, with great alacrity of tongue and generally of pen, to explain what had hitherto eluded the most careful scientific minds.

Fundamental discoveries:- There was, fortunately, a scientific unrest in the minds of a few men, which prompted them to break through the mist and fog which had formerly hung over the question of plant growth and plant nutrition and to make a few bold, though simple, experiments, which went far to establish the science on an experimental basis. In doing this, they were in a way reviving the work of STEPHEN HALES, who had apparently been forgotten in the years which had passed since the publication of his wonderful book on "Vegetable Staticks".

THÉODORE DE SAUSSURE, a native of Geneva, was the foremost man in the new era of plant physiology in the nineteenth century. DE SAUSSURE was born in 1767 and died in 1845, witnessing in his day a profound revolution in the affairs of politics, society, and science. His father was an able physicist, prominent in education and science. THÉODORE DE SAUSSURE had strong literary tastes, was elected repeatedly to the Council of Geneva, and although active in public affairs, never undertook the duties of academic life. Throughout his writings we see evidence of the benefits of the freedom of scientific men at that time in the city of Geneva. DE SAUSSURE was the forerunner of a new school of plant physiology, represented more than a generation later by BOUSSINGAULT, LIEBIG, and SACHS. He knew how to employ quantitative methods in dealing with the problem of plant nutrition, and to draw logical conclusions from his data. His writings, like those of STEPHEN HALES, were characterised by their directness and brevity. He knew how to design his experiments so that the results spoke for themselves.

DE SAUSSURE started with the works of LAVOISIER, INGENHOUSZ, and SENEBIER, but went much further. His great work entitled "Recherches Chimiques sur la Végétation" (1804) contained discoveries which were fundamental for all later work. He showed

(1) that the elements of water are fixed in the plant at the same time as the carbon, (2) that there is no normal nutrition of the plant without the uptake of nitrates and mineral matter, and (3) that the nitrogen in the plant substance comes, not from the air, but from the soil. In his time most people were satisfied that the mineral matter absorbed and found in the ash of the incinerated plant was without significance. DE SAUSSURE corrected their misunderstanding. He showed that when plants were kept in distilled water, they made very little growth. He also found that the roots absorbed substances from solution whether the substances were of any use to them or not, thus contradicting the older view that the roots had the power of selecting from the soil just what they required. He also emphasized the fact, known from the time of HALES, that roots absorb much more water than the plant needs for nutritive purposes, and that the mineral solution taken up by the plant is extremely dilute. He knew that the plant absorbed mineral substances, not in the ratio in which they existed in the soil, but in a very different ratio, and that they might absorb substances which were actually poisonous. DE SAUSSURE's conclusion that plants were dependent on the nitrogen of the soil was confirmed in an unquestionable manner by BOUSSINGAULT, in writings published between 1851 and 1855.

It is curious that the splendid work of DE SAUSSURE invoked no additional studies by his contemporaries. It was not until 1842 that another contribution on the subject of plant nutrition was published in which exact quantitative methods were employed. This was the work of WIEGMANN and POLSTORFF. By means of an unusually refined technique, they proved that when plants were grown in distilled water, they gained nothing in ash constituents. When irrigated with solutions of mineral salts, the plants made good growth, but with distilled water only dwarfed growth. From their work they concluded (1) that plants, which can develop for a time at the expense of the inorganic constituents of the seed, cease growing whenever the supply falls to a minimum; (2) that the inorganic constituents of the plant are in no way to be regarded as products of the life of the plant, neither formed out of unknown elements which make up the organic compounds; (3) that the amounts of the mineral substances present in the plant are not increased by the life processes; all amounts above those which the seed contains are acquired from the external medium.

DE SAUSSURE's trenchant ideas on the selective absorption of mineral constituents began to be studied experimentally about forty years after they were written. TRINCHINETTI confirmed (1843) the conclusion that plants do not absorb indifferently what they find in the soil solution, and added that plants of various species growing in the same soil do not absorb the mineral constituents in the same ratio. It was eventually found that plants require potassium, calcium, magnesium, nitrogen, iron, and the anions nitrate, sulfate, chloride, and phosphate in considerable amounts, but it was a tedious job to eliminate from the list the unnecessary elements.

SALM-HORSTMAR published in 1856 the results of his experiments on plant nutrition, in which he employed a differential culture method, whereby he was able to omit one or more given elements from the nutrient solution. He carried out his experiments in wax-coated tin pots which contained sand, pulverized quartz, and sugar charcoal previously boiled with acids to remove small

amounts of mineral matter. While he obtained much useful information, he was still uncertain about the essential nature of silica, aluminum, and manganese.

The final evidence concerning the necessity of an element or a compound was obtained from experiments with water cultures *i.e.*, solutions of the salts to be tested. This method was first employed by WOODWARD in 1699, who showed that plants grow better in river water than in rain water, but best in the water extract of garden soil. After having been forgotten for one hundred and fifty years, SACHS reintroduced the method in 1860, and it has subsequently proven to have great worth for studies in plant nutrition.

Agricultural chemistry promoted by Liebig:- The related field of agricultural chemistry was the first concerned with questions of plant nutrition. The indisputable proof that plants obtain their mineral nutrients from soils and from nowhere else led the students of the new field of chemistry to explore its possibilities in relation to crop production. The foremost worker in this new field was the eminent chemist, JUSTUS VON LIEBIG, who was born in 1803 at Darmstadt and died in 1873 at Munich. LIEBIG was a pioneer in many departments in chemistry and will ever be remembered for his work in the field of organic chemistry. Rejecting the old idea that plants get their nourishment from humus, he taught that they get their carbon from the carbon dioxide and their nitrogen from the ammonia of the air, while they get other constituents such as potassium, calcium, sulfur, and phosphate from the soil. He believed that the supply of carbon and nitrogen in the atmosphere was inexhaustible, but the farmer must need replenish the minerals which plants remove from the soil. His greatest service to the science of plant nutrition was undoubtedly his overthrow of the theory that plants obtain their carbon supply from the humus of the soil, but with respect to the nitrogen source he was decidedly far from the mark. His idea that the soil was merely a repository of the mineral plant nutrients dominated the field of agricultural science and plant nutrition for a long time. At first it was a useful concept, but later was entirely inadequate for the facts which confronted the student of soil and plant chemistry. His ideas were published in a book on "Chemistry in Relation to Agriculture and Physiology" (1840), and found rather wide acceptance in other countries.

The ideas of a static system imposed by LIEBIG prevailed insofar as the mineral constituents of the plant were concerned. The source of nitrogen was believed to be the ammonia of the air, but convincing proof was not forthcoming. That led to a very uncomfortable situation, because chemists knew that combined nitrogen is necessary and that free nitrogen is useless for nutrition. (See chapter XIV of this book).

Field and plot experiments:- LIEBIG instituted field experiments with a synthetic fertilizer, to demonstrate the correctness of his ideas. The fertilizer was a failure, because he utilized insoluble substances as sources of the mineral nutrients and omitted a form of combined nitrogen which would furnish that element to the plants.

In reply to numerous criticisms which were made, LIEBIG adopted a sarcastic and bitter polemic, especially against the plant

physiologists. They, in turn, exposed a number of LIEBIG's mistakes. The controversy, however, impelled others to take up the subject anew and devote more careful and scientific investigations to the problem. Among these were the famous Englishmen, LAWES and GILBERT, who opened a private laboratory on the land belonging to the former at Rothamsted, and laid out field experiments with certain fertilizers in 1843. These experiments were designed to study the effects of chemical fertilizers on land which was cropped continuously to wheat or barley. As time went on, the investigation naturally widened its scope and involved many other important questions. The yield of wheat on a part of the field to which no fertilizer was added fell off rapidly for a number of years; then reached a point where it fluctuated from season to season without any marked trend one way or the other. The leaders in the technique of plot experiments were BOUSSINGAULT, who conducted work on his estates in France, and LAWES and GILBERT in England.

LAWES and GILBERT stated that, in a general way, the quantity and quality of the produce depended, not only on the selection of the seed planted, but upon the character and amount of manures added. They hastened to add, however, that no hard and fast lines could be laid down with respect to these points. The choice would be influenced partly by the character of the soil, but very much more by that of the climate. When one reads the voluminous reports of the work at Rothamsted, he is impressed with their resemblance to a system of farm bookkeeping in which the debits and credits were meticulously entered. They showed the amounts of fertilizer added to the soil and, after the crop had been harvested, tried to account for it.

Field observations on the effect of fertilizers were gradually undertaken in Germany, in the United States, and in other countries after 1870. In all the crop trials it was implied that the results were designed to guide the farmers of the region in treating their soils. Unfortunately, the ratio of cases in which they were of real help to farmers was small. Equally valuable information could probably have been derived from inspection of the fields of successful farmers. There were many reasons for the failure of the field trials. One was the variability of the soil and the season; another was the lack of sufficient repetition to give reliable average results.

GILBERT, speaking (1884) on agricultural investigations in Europe, said that MAERCKER of Halle reported that field experiments with fertilizers were almost abandoned in Germany. He had concluded that the chemists of the agricultural stations had neither the means nor the technical knowledge necessary for carrying out such experiments successfully; that neither the amount of land nor the funds at their disposal were such as to admit of any safe deductions for application in practical agriculture from the results; and that purely physiological problems could be better investigated in the laboratory or in the greenhouse.

The reliability of the results of plot experiments may be challenged on other grounds. Examination and analysis of thousands of plot experiments which have been carried on in the United States indicate that in the case of corn where a single mineral element is applied to the soil in any of the recognized forms of commercial

fertilizer material, the chances are 2 to 1 that an increase of crop will be obtained. Where a mixture of 2 elements are used, the chances are 6 to 1 that an increase will be obtained, and where 3 or more mineral elements are supplied, the odds are 12 to 1 that an increase will be obtained.

In the second decade of the 20th century there was a great refinement in the technique of field experimentation, impelled partly by the attempt to compute the results of experiments with tree crops.

The appearance of an article in 1906 by HOLTSMARK and LARSEN called attention to the errors of field trials due to the inevitable variations of field results, and they showed how it may be estimated by the use of the standard deviation and the coefficient of

FIG. 26. — The new Rothamsted Laboratories (erected 1914-16), where studies are made on problems of soil science, plant nutrition, etc.

variability. They also showed that the coefficient of variability decreases as the plots are enlarged, but not in direct proportion to the size of the plot.

The next few years saw the appearance of several articles from the Rothamsted Experimental Station, which recorded studies of the soil variations in their experimental grounds and the influence of size and repetition of plots upon accuracy. The work was done largely with the yields of wheat, mangolds, and hay crops. They showed that the reduction in error in field trials increased as the size of the plot increased, but that the reduction is small when the plot is enlarged to a size greater than 1/40 of an acre. The error may be further diminished by increasing the number of plots similarly treated and scattering them about the area under experimentation, but there was not much to be gained by increasing the number of plots above five. In 1910 WOOD and STRATTON showed that the application of the probable error method to questions of sampling for analysis to field experiments and to feeding experiments could yield results of very great value. One of the valuable things in their article was the publication of tables which

showed the number of duplicated plots or number of animals in the feeding trial which must be employed to give any desired precision in the results. They concurred with earlier workers in showing that more accurate results may be obtained by employing large numbers of small scattered plots than by using one large plot. The work of WOOD on this problem is deserving of the greatest recognition, since he was one of the first to give really reliable methods for calculating the probable error of plot experiments.

A somewhat different method of calculating the heterogeneity of the field and its effects upon soil productivity was given by HARRIS in several papers appearing between 1912 and 1915. HARRIS used the correlation method, which seems to be somewhat less useful as a means of obtaining a corrective term than the use of the coefficient of variability and the probable error as used by WOOD and others. Various methods were investigated subsequent to 1915, but the general trend was toward the use of the probable error and the co-variant constant, as derived later by FISHER.

COOMBS and GRANTHAM discussed (1916) the variability in the yields of rice and coconuts, determined the probable errors, and introduced calculations to show the odds that any increase is a real increase.

BATCHELOR and REED studied (1918) the nature of variability in the yields of fruit trees and computed the probable errors of trees individually and grouped in plots. From their calculations it was possible to determine the number of trees in a plot and the number of plot replications necessary to obtain a certain degree of accuracy in ascertaining whether the differences between treated and untreated plots were due to the factors concerned. A difference between two plots of less than 50 percent of the mean production should be considered with caution before ascribing it to differences in treatment.

In cases studied, the coefficient of variability was reduced 50 per cent by calculating the normal yield from the nearest controls instead of using the mean of the entire area.

FISHER showed (1935) the utility of a systematic arrangement of plots, known as the Latin square, for reducing the probable error of experimental treatments. In the Latin square there is one plot of each kind in each row and one in each column. To avoid having plots receiving similar treatments in a line along the diagonal of the square, each row of treatments is moved forward two places instead of one, giving an arrangement which avoids a possibility that the growth of plants may be unduly influenced by uniform changes in soil fertility which might run obliquely across the field.

The application of statistical methods to results which involve the inherent variability of biological material has been of inestimable value in agricultural experimentation. Modern experimental work has been thereby emancipated from many of the limitations which beset the earlier experimenters concerned with field and plot experiments.

After the great initial expansion of the field of soil and plant relationships by BOUSSINGAULT, LAWES and GILBERT, LIEBIG, VILLE, and others, investigations had turned toward analyses and plot experiments. The last three decades in the nineteenth century were marked as a time of confused strivings and halting prog-

ress in soil science, but opened the way for some significant advancements in the twentieth. In LIEBIG's day and for a long time afterwards the role of the chemist in soil studies was merely that of an analyst. The science designated as "Bodenkunde" had not started in 1880. There was no vivifying influence in plant nutrition of a VIRCHOW, PASTEUR, or KOCH.

In the year 1880, just before many new developments in soil and plant relations took place, men had come to know certain important things about the phenomenon of the nutrition of plants: (1) Soils have the ability to support vegetation for an undetermined, unknowable time. (2) Soils are derived from rocks, yet pulverized rock is not soil. (3) Weathering produces important changes in the chemistry of the derived soils. (4) Mineral constituents are necessary for plants. (5) Mineral constituents are obtained from the soil. (6) The mineral nutrients absorbed by plants come chiefly from a fraction of the soil. (7) The osmotic properties of the contents of root cells are related to their ability to absorb water from the soil. (8) The ratio of the mineral constituents absorbed by the plant differs from the ratio existing in the soil. (9) Plant growth is related intimately to rainfall and temperature. (10) Soil amendments sometimes increase plant growth.

Soil fertility:- LIEBIG stated in "Natural Laws of Husbandry" (1863) that the power of the soil to nourish plants is in proportion to the physically absorbed nutritive substances it contains, though the elements held in a state of chemical combination may be utilized when the former supply has been withdrawn by plants. This was perhaps the most satisfactory statement of the phenomenon hitherto formulated. At the time it afforded, to say the least, a working model of the soil. LIEBIG's Law of the Minimum was the formulation of an idea that the yield of a crop was determined primarily by the amounts of plant food which were present in minimum quantities. His idea was discussed later as the Limiting Factor by BLACKMAN and again by MITSCHERLICH as the Law of Physiological Relations. The latter law was expressed as a logarithmic function between yield and the quantity of plant food constituents, which is virtually the Law of Diminishing Returns.

The idea of the soil as a dynamic system was slow in emerging. So far as soil science was concerned, the memorable work of CHARLES DARWIN on the activities of earthworms was regarded as a scientific digression more appropriate for leisure reading than for the announcement of a principle of soil metamorphosis. When at length the soil-water system began to be investigated by physical chemists, the concept of a changing equilibrium was precisely formulated as the basis for demonstrating the dynamic nature of the soil.

The general neglect of the principles of plant physiology and of plant geography on the part of agricultural chemists is amazing. The water relations of plants and soils, so extensively studied by plant geographers, could have been of great help in agriculture; indeed, they had been more or less perfectly understood for a long time by herdsmen and root-diggers. Finally, HILGARD, a man trained in botany and chemistry, gave (1892) an illuminating discussion on the relation of soils to climate. For breadth of

view and wealth of information, HILGARD's work cannot be surpassed, yet it is painful to note how little influence it had at the time on investigations in plant nutrition.

Eventually the mineralogy of the soil received long overdue attention. The conclusion reached has been frequently verified; namely, that soils are much more heterogeneous than rocks, and that practically every soil contains all the common rock-forming minerals. The formulation of the concept of the soil as a dynamic system took place at the very beginning of the twentieth century and liberated soil science from the domination of LIEBIG.

MERRILL's treatise on the genesis of soils and the role of natural agencies in soil formation, published in 1897, is a landmark in the development of modern soil science. In his treatise he comprehensively described the chemical, mechanical, and biological factors which act continuously upon the lithosphere, converting the mineral aggregate into a mantle of soil in which the roots of plants can grow.

The dynamic nature of the soil:- The phenomenon of base exchange in soils, involving some sort of chemical combination between ions and soil colloids, was discovered in 1852 by WAY, the English chemist, who observed that soil which absorbed ammonia from stable manure lost an equivalent amount of calcium, and concluded that the soil silicates were involved. The matter attracted some attention at the time, but no notable advance occurred until GEDROIZ began publishing papers which dealt with the effects of the salts in the soil solution upon physical and chemical reactions of soils. GEDROIZ discovered (1918) that there are differences in the readiness with which soils absorb different ions. For example, the potassium ion is a somewhat more powerful replacer than the sodium ion and is more readily absorbed by the clay. He also found that the ions of the alkaline earths most readily absorbed are not necessarily the most firmly held against leaching, but other reactions may be involved. Agriculturists had known for some time that potassium fertilizers applied to soils promote the loss of calcium.

HISSINK gave (1920) a clear exposition of the replacement process in soils, emphasizing the rapidity with which the equilibrium between ions is attained. He concluded that there is a reaction between the salt solution and the easily accessible or surface particles of the clay-humus complex, and that the replaceable kations are adsorptively bound to the adsorbing soil particles.

KELLEY, DORE, and BROWN have advanced (1931) the very plausible idea that easily replaceable ions like calcium are held on the outside of the crystal-lattice of the clay particles and hence are readily exchangeable. Others like magnesium and potassium are held on the inside of the lattice, and since it is not sufficiently open to allow egress to the kations, they are not readily exchangeable unless the lattice is broken by grinding the clay, but some potassium and magnesium important for plant nutrition are exchangeable.

The properties of soils to exchange bases, discovered by GEDROIZ in Russia, KELLEY in California, HISSINK in Holland, and DE 'SIGMOND in Hungary, have elucidated important questions dealing with soils of high salt content. They have also demonstrated that

the absorption or precipitation effected by the reactive bodies is accompanied by the exchange of an equivalent amount of base, and have concluded that the reactive constituents of the soil are compounds of alumino-silicic acid, which form a large part of the colloidal material.

WHITNEY and CAMERON, of the United States Department of Agriculture, discussed the chemistry of the soil in relation to crop production in two important papers published in 1903 and 1904, in which emphasis was laid on the dynamics of the soil solution. After discussing the results of a vast number of soil analyses, which included soils from many parts of the country and soils of various origins, the authors wrote the following statement, which was then at variance with preëxisting ideas:

"From the results of the other investigations described and the figures given in the preceding tables, the conclusion seems inevitable that all our principal soil types, in fact, practically all cultivable soils, contain naturally a nutrient solution which varies within comparatively narrow limits with regard either to composition or concentration and which is usually sufficient for plant growth. Apparently, therefore, all these soils are amply supplied with the necessary mineral plant foods, and these plant foods are not in themselves a matter of such paramount importance to the agriculturist, for their supply as regards the plants is determined by the supply of soil moisture which the crop can obtain from the soil. The chemical analysis of the soil can not in itself, therefore, throw much light upon the problem of fertility, but, when attempting to control the factors governing crop yield, attention must be directed to the mechanical condition of the soil as affecting the supply of soil moisture, with its dissolved mineral nutrients, to the effects of climate, to rotation, etc.". (Bureau of Soils, Bulletin 22, 1903).

CAMERON developed (1911) the fundamental ideas of the soil solution considered as a liquid phase, wherein the roots find ions which they may absorb. He showed that the commonly occurring minerals of the soil are far more soluble than had been assumed, and that the dissolved substances reach a more or less constant concentration. He emphatically stated that no soil is ever in a state of final equilibrium, because of the effects of manifold physical and chemical factors.

These papers attracted great interest among students of soils and plants and provoked animated discussions for several years after their publication. The broad generalizations expressed by WHITNEY and CAMERON were subjected to scathing criticism by their contemporaries, and certain erroneous concepts were later corrected. They stimulated, however, new and important researches on the nature of the soil solution.

Further studies conducted in the Bureau of Soils at Washington led to the discovery that the infertility of some soils is due, not to a lack of nutrients or to unsuitable physical conditions, but to the presence of deleterious organic compounds. An improved growth of plants followed diverse treatments, which added no nutrients but counteracted, when they did not remove, the deleterious organic compounds. Treatment of the extracts of such soils with finely divided solids, such as ferric hydrate or carbon black, adsorbed and removed the growth-inhibiting substances, with consequent improvement of their ability to produce good plants. The removal of such substances by adsorption often enhanced plant growth more than the addition of nutrient salts to the aqueous soil extract. SCHREINER and SHOREY isolated from unproductive

soils, picoline carboxylic acid and dihydroxystearic acid, both of which, when tested experimentally, proved to be toxic to plants.

WHITNEY and his associates also developed a useful technique for growing seedling plants in aqueous extracts of soils. They showed that the plant-producing efficiency of the extracts was in general similar to that of the soils from which they were prepared.

BURD and STEWART discussed (1918) the value of water extracts of soils as criteria of their efficiency to promote plant growth. The dynamic nature of the soil and the secular changes in the soil solution were then studied by BURD and MARTIN. By use of a technique for displacing the soil solution, they demonstrated the importance of biological factors in controlling the amounts of dissolved materials in the soil solution. The anions NO_3, SO_4, and HCO_3 have a biological origin, and equivalent quantities of kations must, *pari passu,* enter the solution. They obtained, moreover, from certain soils, by displacement, solutions which closely approximated in constitution the soil solution as it existed in those soils at moisture contents suitable for plant growth.

The relation of chemical composition of the plant to the stage of growth attracted the attention of workers in America and Germany, who showed that there were very definite changes with age. LIEBSCHER reported (1887) that with the onset of senility, some of the mineral constituents were lost from the plant to the soil. He thought that the losses were mainly from dying plant members. WILFARTH, RÖMER, and WIMMER made (1905) an elaborate study of the composition of barley, wheat, and potatoes at successive stages of their growth. They showed that barley absorbed most nitrogen and potassium before the heads were developed and subsequently lost it, although when nitrogen was calculated as total nitrogen per plant, the fluctuation in that element was less conspicuous. The maximum amount of phosphate in the plant was found at the time the heads were formed and diminished relatively slightly thereafter. It will evince no surprise to learn that they found that the fluctuations in mineral constituents were different in potatoes from barley or wheat. The amounts of potassium, sodium, nitrogen, and phosphates extracted from the soil by potatoes were greatest near the close of the growing season. They were perhaps the first to call attention to the "luxury consumption" of nutrients by plants, a condition which came to be more adequately recognized later. For example, barley uses a great excess of nutrients at the time of most intensive growth and subsequently, after that period has passed, remits part of them into the soil by one means or another.

JONES and HUSTON reported (1914) that maize showed a period of very rapid absorption of potassium eight weeks after germination, just prior to the initiation of head formation, followed by a long period of slow absorption, succeeded in turn by a rapid absorption during the sixteenth, and finally by an absolute loss in the seventeenth week. The maximum period of absorption of nitrogen in the same plant was in the eighth and the sixteenth weeks, with an intermediate period of minimum absorption.

Gradually it became evident that the requirements of the plants and the supplying powers of the soil are beset with numerous inherently complex interrelations. Several American investigators have shown that plants can adapt themselves to quite a range of

changing conditions before they show the effects of deficiencies or excesses. A great advance was made when HOAGLAND and DAVIS showed the dependence of absorption of mineral elements on light, through which the plant can manufacture substances capable of furnishing energy for the process.

HOAGLAND and MARTIN, in concluding (1923) a discussion of studies on absorption in sand and solution cultures, wrote:

> "Plants have great powers of adaptation to different cultural conditions. It is not at all necessary that some specific solution be provided. The essential condition of good growth, as far as the mineral elements are concerned, is that the concentration of each element be maintained above its critical level. The culture solution must be replenished as absorption of ions by the plant proceeds, in order to maintain the concentration of any essential element above its critical concentration. Finally, the conditions of light and temperature are of paramount importance in determining the adequacy of concentration of any essential element". (Soil Science 16:386).

Soils contain both free and combined hydrogen ions, but it was impossible to determine them successfully until 1909, when SÖRENSEN perfected a new method by which both the free H-ions and the buffer substances can be determined. HOAGLAND showed (1917 and 1919) how the concentration of H-ions affected the growth of barley plants in nutrient solutions, and OLSEN (1921) determined how it affected the growth of other species. The physiological action of the free H-ions is considerable, but the influence of the buffer substances is more indirect and attains significance when a soil is exposed to influences which tend to change the hydrogen-ion concentration. LUNDEGÅRDH and other Swedish investigators have studied the relations between hydrogen-ion concentration of the soil and ecological phenomena. There is now less emphasis laid on this factor than was common in the second decade of this century.

When chemists fully realized the complex physical-chemical relations of the solid phase of the soil and the liquid aqueous phase, with the powers of base-exchange superposed, it was evident that the older ideas on "availability" were untenable. BURD introduced (1918) the useful concept of the "supplying power" of the soil, designating therewith the rate at which ions can be delivered to the plant roots. A very dilute solution, accordingly, could afford enough nutrients, if the supplying power were adequate. For example, the absolute amounts of potassium, or of phosphate, might not be adequate at any one moment, yet they could suffice if the supplying power were adequate. A very dilute solution could afford enough nutrients, provided it were accessible to the roots, or if the concentration could be fairly constantly maintained, or if there were opportunity for roots to spread and develop a large absorbing surface.

The formulation of the concept of the soil as a dynamic system took place at the very beginning of the twentieth century and liberated soil science from the domination of LIEBIG.

The first three decades of the twentieth century have obviously been a time of great advance in the knowledge of soil and plant relationships. Some of the major problems have been successfully attacked and solved by the concerted efforts of chemists, physiologists, bacteriologists, and others. The plant has been induced to answer questions which baffled and puzzled our predecessors.

Analytical work was not sufficient. The classical generalizations of LIEBIG were not sufficient. New and venturesome methods of experimentation have been developed. Out of them has come a new conception of the dynamic nature of the soil, which, coupled with the discovery of methods for the artificial fixation of nitrogen, has banished the age-long fear of famine. Agricultural yields may not only be maintained but increased.

Equilibrium factors in the accumulation of salts by plant cells:- The attention of investigators early in the present century was drawn to the very unequal absorption of ions by plants from the nutrient solution. PANTANELLI and SELLA demonstrated (1909) the very unequal absorption of ions by *Cucurbita pepo.* Generally the anion was absorbed in excess of the kation. HOAGLAND showed (1918) that barley absorbed more nitrate than sodium from sodium nitrate solution, but that the two ions of potassium chloride were absorbed by this plant in equivalent amounts. Miss REDFERN showed (1922) that peas and corn absorbed an excess of the kations from calcium chloride solution. A multitude of physical and chemical theories were advanced to explain the phenomenon, but scant reference can here be made to them. Many of the conclusions were based on considerations which left out the plant in their attempt to avoid teleological implications. Some of the theories were so perfect that they precluded the possibility that salts which once got into a cell or into the protoplasmic wall should ever escape into the translocation stream.

The acquisition by plant roots of solutes from a dilute solution attracted the attention of physiologists at an early date, but it was not clearly explained. The theory that ions are adsorbed on colloids or precipitated in the cell sap, or the theory of the Donnan equilibrium as applied to this problem, could not be verified.

The main difficulty in the problem has been just this neglect of the plant and its power to expend energy. STEWARD was perhaps the first to call attention to the relations between respiration and salt accumulation.

Salt accumulation is not simply the penetration of salts or ions into the protoplasm, but the accumulation of ions in the vacuolar sap. "This means", said LUNDEGÅRDH (1934), "that the attraction between the charged particles of the protoplasm and the salt ions is eliminated somewhere in the cell, which postulates energy supply".

HOAGLAND and DAVIS showed (1923 and 1926) that plants like *Nitella* and *Chara* absorb ions from the external solution against concentration and activity gradients. Factors which determine the condition of equilibrium for different ions vary rather widely. The hydrogen-ion concentration of the external medium specially affected the absorption of nitrates. Potassium, chlorine, and sodium had higher factors of concentration than sulfate, calcium, or magnesium. Ions may penetrate into a cell against a gradient, and nearly all the ions present in the cell sap existed in the ionic state. The insoluble or combined elements found in the cell wall or protoplasm, included calcium, magnesium, sulfur, silicon, iron, and aluminum. *Valonia* accumulated potassium in amounts greater than other ions. HOAGLAND and DAVIS emphasized that the process of salt accumulation seems to be a general attribute of living plant

ls in a state of active growth and metabolism, and that energy əxpended in the process. STEWARD showed that salt accumula- n by storage tissues of potatoes and carrots was dependent upon tabolic activities of the plant cell associated with aerobic respira- n and reflected in the carbon dioxide production, and also upon potentiality of the cell for growth. The amount of salt accumu- əd, however, bore no stoichiometric relation to the amount of $_2$ liberated by the accumulating cells.

HOAGLAND and BROYER demonstrated that young growing roots, :h available carbohydrates at their disposal and suitably aerated, ı accumulate certain ions (for example, potassium, bromine, orine, nitrates) with remarkable rapidity, provided that the t cells — the cortical cells are primarily involved — have not ained what may, for convenience, be designated as a "high t" condition; that is, a concentration of salts in the vacuoles resenting some sort of steady state, which retards or prevents ther accumulations, except as new growth occurs or as salt viously accumulated is translocated to the shoots.

The importance of oxygen supply for the absorption of salt is t as great in the soil as in the solution cultures. SCHREINER l REED showed (1908) that fertile soils have greater oxidative vers than infertile soils, and LOEHWING showed that soil aera- ı promotes plant growth and mineral absorption.

REFERENCES:-

:TON-WRIGHT, E. C. (1933): Recent advances in plant physiology. Ed. 2, Churchill, London.

ISSINGAULT, J. B. D. (1860): Chimie agricole.

:NCHLEY, W. E. (1927): Inorganic plant stimulants and poisons. Longmans, Green, London (etc.).

ɪERON, F. K. (1911): The chemistry of the soil solution. Easton.

.PEK, F. (1920): Biochemie der Pflanzen, Bd. 2. 2. Aufl., Fischer, Jena.

SAUSSURE, T. (1804): Recherches chimiques sur la végétation. Nyon, Paris.

.GARD, E. W. (1904): Soils. Macmillan, New York.

BIG, J. VON (1846): Die Chemie in ihrer Anwendung auf Agricultur und Physiologie. 6te Aufl., Vieweg, Braunschweig.

:W, O. (1903): The physiological role of mineral nutrients in plants. U. S. Dept. Agr., Bureau of Plant Industry, Bull. 45.

ɪDEGÅRDH, H. G. (1930): Klima und Boden. Fischer, Jena.

:RILL, G. P. (1897): Rocks, rock-weathering and soils. Macmillan, London.

.LER, E. C. (1938): Plant physiology. Ed. 2 (with bibliography). McGraw-Hill, New York and London.

ɪSELL, E. J. (1937): Soil conditions and plant growth. Ed. 7, Longmans, Green, London and New York.

'HS, J. VON (1887): Lectures on the physiology of plants. Clarendon Press, Oxford.

M-HORSTMAR (1856): Versuche und Resultate über die Nahrung der flanze. Braunschweig.

.LFARTH, H., RÖMER, H., und WIMMER, G. (1906): Über die Nährstoffaufnahme der Pflanzen in verschiedenen Zeiten ihres Wachstums. Landw. Versuchsst. 63:1-70.

Chapter XVII.

MINERAL CONSTITUENTS IN METABOLISM.

DE SAUSSURE showed that the ash analysis of a plant was an unreliable index of its needs, since it absorbed many things of no use and often substances which were toxic. The desire to ascertain the nutritional requirements of agricultural plants was a strong incentive to study this question, but little progress was made until SACHS in 1860 perfected the forgotten technique of water culture. The successes and failures following the introduction and use of chemical fertilizers as soil amendments in the nineteenth century naturally turned attention to the problems of plant nutrition. The insistence of the agricultural chemists upon investigations mounted as cases multiplied in which the application of fertilizers produced no increase in plant growth. Slowly at first, the plant physiologists began to unravel the tangled story of how plants are nourished. Knowing that certain elements were essential for plant growth, it was reasonable to assume that each had some specific function which could not be performed by another element.

Phosphorus:- VILLE appears to have been one of the first investigators to show (1861) that phosphorus is necessary for all plant growth. Although his experiments were performed with sand cultures, they showed such definite results that there can be no doubt of his conclusions. He also showed that, in order to serve as a plant nutrient, the phosphorus must be in the form of phosphates. Field observations long ago established that phosphates promote root growth. Phosphate fertilization is effective for the growth of root crops such as beets, turnips, and swedes. The recurring statement that arsenic salts might perform the function of phosphates in the plant was finally refuted by STOKLASA and by MOLISCH in 1896. BERTHELOT and ANDRÉ reported (1888) that the relative amounts of phosphorus in *Amarantus caudatus* were greatest in the young plant and decreased to maturity. WILFARTH and associates (1905) and BURD (1919) found that the amount of phosphates in barley straw decreased as the plant matured, and that the relative amount in the grain greatly increased during the process of ripening, indicating that the amounts of nuclein-phosphorus increased at the expense of water-soluble phosphorus in the straw. REED (1907) found that phosphates were necessary for the utilization of starch in *Spirogyra,* and that in its absence starch was transformed (if at all) into unusual forms of carbohydrates. Nuclear and cell divisions were inhibited in the absence of phosphates, but were promoted by adding a few drops of a solution of the salt to the culture. KOCH and REED showed (1907) that the phosphorus of the vitally important nucleo-proteins showed practically no decrease when cells were grown with a minimum amount of phosphates, but that the water-soluble forms of organic and inorganic phosphorus showed relatively great decrease.

The accelerating effect of phosphates on alcoholic fermentation

by yeast juice was observed (1903) by BUCHNER who assumed that it was due to their alkalinity. Living yeast cells contrariwise maintain a high rate of fermentation and do not respond to the addition of phosphate. HARDEN and YOUNG showed (1906) that phosphates have an important role in fermentation and that their presence is absolutely essential for the phenomenon in yeast juice. They may be considered as a co-enzyme of zymase. HARDEN and YOUNG demonstrated that a definite chemical reaction involving sugar and phosphate occurs when a soluble phosphate is added to a fermenting mixture of hexose with yeast juices, maceration extract, dried yeast, or zymin, resulting in the production of an equivalent amount of carbon dioxide and alcohol and a hexosephosphate.

The equation for the reaction has been written:

$$2\ C_6H_{12}O_6 + 2\ PO_4HR_2 = 2\ CO_2 + C_2H_6O + 2\ H_2O + C_6H_{10}O_4\ (PO_4R_2)_2$$

Regardless of the nature of the sugar used for fermentation the hexosediphosphate formed is always the same and is fructosediphosphate. ROBISON's results showed (1922) that the process is more complex than had originally been supposed. He found that if either glucose or fructose were fermented by yeast a hexosemonophosphate was formed in addition to the hexosediphosphate. HARDEN and HENLEY, as a result of later studies, concluded (1927) that the diphosphate, originally described, is formed according to the equation, but that a part of it is subsequently hydrolyzed with the formation of a monophosphate.

Sulfur:- From the time of LIEBIG it has been known that sulfates are necessary for plant growth. The experiments of BIRNER and LUCANUS, employing water cultures, emphasized (1866) the importance of sulfates in comparison with other sulfur compounds. Fungi and bacteria may, however, utilize various compounds containing sulfur. BERTHELOT and ANDRÉ, from an investigation of the sulfur absorption during the growth period, reported (1891) that the quantity absorbed steadily increased up to the period of blossoming of annual plants. Comparatively little information has been obtained on the functions of sulfur compounds in plants. GOLA, who employed the sodium nitroprussid reagent, reported (1902) that cystein was present in the apical meristem of shoots and roots. Mrs. HURD-KARRER showed (1935) the remarkable effects of sulfur in counteracting the toxic action of selenium in plants. She showed that 36 parts per million of sulfur as sulfate could overcome the lethal effect of 3 parts per million of selenium for wheat plants in water cultures. MILLER and others have shown (1919) that plant growth on many soils is often limited by the quantity of sulfates present. The growth of leguminous plants is often greatly enhanced by the application of sulfates, as well as by elemental sulfur, but the story is complicated by the manifold relations of soil microörganisms to sulfur, through which the solubility of certain soil minerals may be increased as the result of an increased supply of hydrogen ions.

Calcium:- Aside from the earlier ideas upon the value and function of nitrogen in the plant, the first ideas upon the specific functions of any one of the elements appear to have been advanced

by STOHMANN in 1862 on the functions of calcium. He concluded that calcium was necessary for the formation of the green parts of plants, since, when he cultivated corn plants in solutions lacking calcium, the leaves died at the tips. After the addition of a small amount of calcium salt, the plants quickly took on new life and began forming leaves and shoots. W. WOLF appears to have discovered (1864) incidentally that calcium salts had a stimulating effect on root growth. It has since been shown that other salts will produce the same effect, but WOLF's discovery appears as one of the first attempts to explain the unknown but beneficial effects of calcium salts on certain soils. SCHIMPER, in 1888, concluded from a study of the green parts of plants, that the principal function of calcium was to precipitate oxalic acid and soluble oxalates. KELLEY and CUMMINS found (1920) that calcium-starved leaves of citrus trees are considerably more acid and contain distinctly less calcium than normal leaves. In opposition to this idea, KRAUS adduced evidence (1897) that the importance of calcium does not depend primarily on its power to precipitate soluble oxalates, since some plants are able to tolerate their presence in the tissues. REED and HAAS observed (1923) that calcium is necessary for processes of protein synthesis and growth in the young leaves of citrus trees. Potassium could not perform the functions of calcium. When the calcium supply fell far below the optimal amount, the foliage was prematurely shed; the shoots died back after making a short growth, resulting in the condition known as multiple buds. The calcium in the trunk and large roots was relatively immobile and was not useful to the shoots and root extremities. The importance of calcium for growth and spore formation in *Aspergillus* and *Penicillium* was demonstrated by DAVIS, MARLOTH and BISHOP in 1928. Spore formation was dependent upon calcium.

In 1892 OSCAR LOEW ascribed a highly important function to calcium, regarding it as one of the important mineral bases which enter into the constitution of the proteins composing the cell nucleus and plastids. According to his interpretation, these proteins take up magnesium in the absence of calcium, and the resulting magnesium-protein compound has not the same well-defined capacity of imbibition which the calcium-protein bodies possess; hence the harmful effects observed by all workers when plants grow in a calcium-free medium which contains magnesium. This deduction prevailed and stimulated work for upwards of two decades. In 1905 VON PORTHEIM and SAMEC obtained results with *Phaseolus* plants which afforded some support for LOEW's theory. They found by analysis that plants grown in solutions lacking calcium had a much greater proportion of magnesium than the normal plants.

Magnesium:- BOEHM began the study of the specific effects of calcium and magnesium on plants. He discovered (1875) the toxic effects of magnesium salts on plants growing in solution cultures, but it remained for VON RAUMER to show (1883) the antidoting power of calcium for magnesium and the ratio of the two elements for the best growth of plants. He observed that *Phaseolus* plants suffered characteristic injury when grown without magnesium. After reaching a height of about one meter, the internodes ceased to elongate. The new leaves remained small and were chlorotic.

The prolonged investigations of OSCAR LOEW on magnesium and its functions in plant nutrition produced some important results. In discussing (1892) the role of magnesium in the plant, he concluded that one of its functions was to serve as a carrier for phosphoric acid since magnesium, like phosphorus, accumulates in the seed. Considering the rapidity with which magnesium salts are dissociated, LOEW believed that they would present the phosphoric acid radical in a form favorable for assimilation. The result of numerous analyses can be cited to show that magnesium is usually abundant in the plant where nucleo-proteins are being formed. If magnesium has such a function, it is evident that a small quantity could be used repeatedly as a carrier of phosphoric acid in the plant. BOKORNY duplicated most of LOEW's results and showed that magnesium is necessary for the development of nuclei and chloroplasts. BERNARDINI also concluded (1914) that magnesium is important for the nutrition of the embryo and of very young shoots, because it serves as a vehicle for the transfer of phosphoric acid. Having learned that magnesium is essential for growth but is often toxic, physiologists, under the leadership of OSCAR LOEW, at the end of the last century, formulated an hypothesis that there should be a certain ratio of calcium to magnesium for optimum growth. After a searching review of the evidence of many workers, LIPMAN failed to find (1916) conclusive evidence in support of the calcium-magnesium ratio; rather, it seemed that there is some other more reliable interpretation.

Knowing that magnesium is a constituent of the chlorophyll molecule, it was no surprise to discover that a deficiency of that element should cause chlorosis. REED studied the behavior of *Spirogyra,* which he cultivated in magnesium-free solutions, and reported (1907) that the development of chlorophyll was inhibited. *Vaucheria* cultivated in magnesium-free solutions contained none of the characteristic oil globules. GARNER and associates discovered (1923) that "Sand Drown", a chlorosis of tobacco in South Carolina, was cured by applications of magnesium. REED and HAAS reported (1924) a specific type of chlorosis of orange leaves due to magnesium deficiency, which is characterized by a narrow chlorotic strip on each side of the mid-rib.

Potassium:- BIRNER and LUCANUS, experimenting with oats in water cultures, gave the first proof (1866) that potassium is indispensable for flowering plants and cannot be replaced by other metals of that group. HELLRIEGEL extended (1867) and confirmed these observations, but NOBBE (1870) seems to have been the first to point out the necessity of potassium for the formation of carbohydrates in plants. RUSSELL emphasized (1932) the relation of potassium to leaf efficiency, and observed that it may explain why application of potassium to plants is so beneficial in cold, wet seasons.

For many years there was uncertainty concerning the role of potassium, though the majority of workers confirmed NOBBE's conclusion that it was necessary for the formation of carbohydrates. WILFARTH concurred (1905) in this view and observed that the barley plant apparently uses the carbohydrate primarily for building up the most extensive plant body possible and, when completed, begins filling out the various parts and members.

In 1904 MACALLUM's successful use of microchemical methods enabled him to demonstrate that the walls of fibrovascular elements are rich in potassium, and that it is present in particular regions of the protoplasm of the green cell but absent from the nucleus. He concluded that it is important in the growth and formation of the cell wall, because it was abundant in the apical region of growing rhizoids and pollen tubes, and agreed that potassium is in some way connected with the process of photosynthesis. PENSTON also used (1931) microchemical methods for studying the distribution of potassium in the potato plant. Finding that the element was more abundant in regions of greater physiological activity, he supported the idea that potassium is important for protein metabolism. The positive association of potassium and starch was not established, though potassium was more abundant in palisade cells of leaves and in probable association with the process of carbon assimilation. GASSNER and GOETZE reported (1934) that the efficiency of potassium in nutrition depends upon age, light, and nitrogen and must be investigated only when none of these other factors are limiting. They concluded that the effects of potassium and nitrogen on protein synthesis are of such fundamental importance that their roles must be considered together. High levels of potassium and low levels of nitrogen produced similar effects upon protein content, chlorophyll content, rates of assimilation, and respiration.

Iron:- GRIS demonstrated (1843 and 1844) experimentally that in an iron-free medium leaves were chlorotic and plants made little growth, but they recovered in a short time if a few drops of a solution of an iron salt were added to the medium, or if a dilute solution were applied to the leaves. This discovery has been confirmed and the work extended by many investigators. It was thought by some that iron was a component of chlorophyll, but careful analyses showed that this is not the case. In some way not yet understood, iron catalyses the production of chlorophyll. GERICKE reported (1925) that plants grown in light of high intensity required more iron than when grown in weak light. The necessity of iron for fungi, which had been observed by RAULIN (1869), was emphasized when JAVILLIER and SAUTON found that it was needed not alone for growth, but for conidia production of *Aspergillus*. MACALLUM and others, who used his microchemical methods, discovered (1891) that iron occurs in the chromatin of the nucleus, and others found it in the embryo of the barley grain.

MICRO-ELEMENTS

Within the last half-century, the role of infinitely small factors has become important in the whole field of biological investigation. Plant physiologists have discovered the necessity for elements which were formerly disregarded because, in truth, most of them are toxic to plants, even in small quantities. It is now conceded that the success of most of the early water-culture experiments with plants was due to the presence of micro-elements in supposedly pure chemicals by which the needed amounts were inadvertently furnished.

The nutrition of algae and fungi was intensively studied at an early date since for these plants it is a relatively simple matter to

maintain uniform cultural conditions. In 1860 PASTEUR first cultivated fungi in solutions of definite composition. Subsequently his pupil RAULIN studied the value of certain mineral compounds (including copper and zinc) for the growth and reproduction of fungi. Some physiologists framed an idea that these otherwise toxic compounds might act as "stimulants", provided the concentration was sub-lethal, but that concept was eventually dropped.

Boron:- The importance of boron for plants was demonstrated in 1910 by AGULHON, whose results indicated that it is an essential element for the seed plants. His experiments showed that different species reacted differently toward boron, but for each there was an optimum which favored the growth and yield of the plant. Boron in larger amounts, however, reduced the chlorophyll and checked root development.

From 1914 to 1918 the manufacturers of chemical fertilizers were often obliged to use potash from unusual sources, some of which contained boron in amounts sufficient to be detrimental to vegetation. The problem awakened interest in the whole subject of the relation of boron to plants. Many papers on the subject appeared following 1920. It was found, incidentally, that small amounts of boron might be beneficial to the growth of plants. Miss BRENCHLEY and associates at the Rothamsted Experimental Station concluded that small amounts of boron are important for the development of nodules and the growth of legumes, but that other plants may thrive without it. SOMMER and LIPMAN showed, however, that boron is generally essential for the complete development of all plants. JOHNSTON and DORE demonstrated (1929) that the addition of .5 parts per million of boron to the nutrient solution was essential for the normal growth and development of the tomato plant. Boron-deficient plants contained more total sugar and starch in their leaves and stems than normal plants, a condition believed to be due to the breakdown of the conducting tissues, thus reducing their ability to translocate sugar. In the same year, MCMURTREY found that boron was essential for the development of tobacco plants, and HAAS established the necessity of boron for the healthy growth of lemon trees. When boron was deficient there was a gradual reduction in the size of shoots, resulting sometimes in the formation of multiple buds and split leaf veins. When a small amount of boron was added to the culture solution, the total sugar content of the leaves diminished and the plant appeared to recover from the former injury.

SCHARRER and SCHROPP found that a characteristic heart-rot and dry-rot of sugar beets was remedied by the application of small amounts of boron to the soil. In 1934 DE HAAN also found great improvement in the growth of sugar beets and in the yield of sugar following the application of boron to soils. O'BRIEN and DENNIS found likewise that boron is efficient in preventing a disease of swedes (turnips) which occurs in Scotland and other countries (Fig. 34). In very recent years boron has been found a specific for the control of cork-spot in apples and many other abnormal conditions in plants.

Copper:- The effect of copper salts on leaves was observed originally in connection with the results of spraying plants with

copper-lime fungicides. RUMM compared (1893) the tissues in sprayed and unsprayed grape leaves, finding differences in width so small that they cannot be regarded as significant. The palisade parenchyma cells of the sprayed leaves contained, nevertheless, a greater number of chloroplasts, although their average size was somewhat smaller. BAIN reported (1902) that the deposit of copper salts on leaves affected the formation of starch in the underlying tissues. Grape leaves showed the greatest benefit from copper sprays, followed by the apple and finally the peach, which is rarely benefited by spraying under normal conditions. FORBES' study of the effects of copper salts in irrigating waters and soils demonstrated (1917) that copper salts were absorbed by the roots and he traced the channels through which they traversed the plant, and their accumulation in the meristem. He showed that

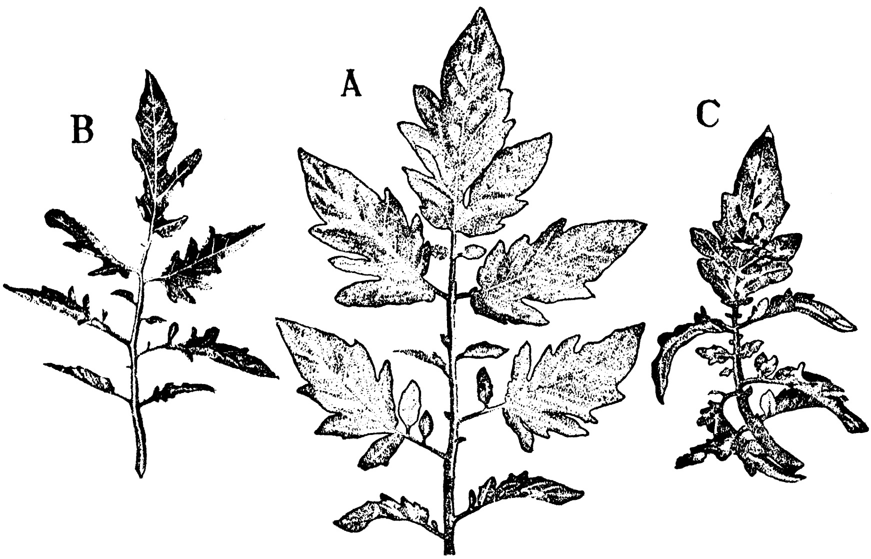


FIG. 27. — Tomato leaves exhibiting deficiencies of micro-elements. A, Healthy; B, minus copper; C, minus zinc. Drawn from a photograph by ARNON and STOUT.

when very small concentrations of copper salts were present, the growth of the plant was enhanced. SOMMER reported in 1931 that experiments on the growth of various plants in water-cultures showed that copper was necessary for the complete growth of the plant. In the same year LIPMAN and MACKINNEY showed that barley plants seemed to be unable to produce seed without a small quantity of copper in the root medium. Exanthema of trees is often cured by the application of copper sulfate to the soil or to the tree, but the way in which it acts is not well understood, though it has been investigated by numerous workers. OSERKOWSKY and THOMAS reported (1933) that normal pear leaves from localities where the trees were free from exanthema contained from two to four times as much copper as those from exanthemous trees. ALLISON, BRYAN and HUNTER found (1927) that the addition of copper to plants on the muck soil of the Florida Everglades was necessary for the growth of corn and cowpeas, which, without copper, make very abnormal growth.

The importance of copper in biological oxidations was demonstrated in 1937 by KUBOWITZ who showed that polyphenol oxidase is a copper protein complex. The protein system, free of copper, is inactive and up to the optimum, the activity is proportional to the copper content.

Manganese:- For over a quarter of a century, attention has been devoted to the possible use of manganese as a nutrient for plants. Some of the early work gave uncertain results because of the fact that the iron salts used were almost invariably contaminated with manganese. It is only under special conditions that one can obtain iron salts free from a considerable amount of manganese.

Fairly clear-cut results were obtained from the application of manganese compounds to nutrient solutions for the growth of the lower organisms. In 1911 BERTRAND and JAVILLIER reported the results of experiments in which *Aspergillus* was grown on solutions with or without manganese sulfate. They showed that the dry weight of the fungus, as well as its ash content, increased with the increased concentration of manganese, up to a thousand milligrams per liter. OLARU made experiments on the effect of manganese on the nitrogen-fixing bacteria from the root nodules of leguminous plants, showing (1915) that a concentration of 1 part of manganese per 50,000 of nutritive medium gave increases in the amount of nitrogen fixed in all cases.

The importance of manganese as a nutrient for plants has been investigated by MCHARGUE since 1914. He found that leguminous plants are apparently more sensitive than non-legumes to the lack of manganese. In later work he came to the conclusion that, since tomatoes, oranges and lemons were found to contain appreciable amounts of manganese, there is a relationship existing between manganese and vitamins in plant and animal tissues. In 1932 HAAS reported a peculiar type of chlorosis of citrus leaves when the trees were grown without manganese. Manganese-starved plants suffer from abscission of the young leaves and death of the shoots. The roots remain healthy in appearance, even though manganese is deficient for top growth. SCHARRER and SCHROPP published in 1934 the results of an extensive series of experiments in which small amounts of manganese were applied to plants in sand and water cultures. Within the range of beneficial concentrations there appeared to be two maxima, more distinct in the water than in the sand cultures. In the absence of iron there was more injury to maize than when both iron and manganese were omitted. ARNON discovered (1937) that the addition of small amounts of manganese to media in which ammonium was the source of nitrogen, greatly increased the growth of barley plants.

A disease of oats long known as Grey Speck has been found to be a manganese-deficiency disease. SAMUEL and PIPER found that manganese is an essential element for plant growth and a specific remedy for the Grey Speck disease. DAVIES and JONES showed in 1931 that manganese sulfate, applied either before or after sowing oats, gave complete control of the Grey Speck and stimulated slightly the seedlings. No seed transmission of Grey Speck was obtained, although all plants grown on an affected area showed marked reduction in yield and a lowering of the percentage of well-filled grain.

Zinc:- The earlier agricultural chemists showed that the ash of some plants contained appreciable amounts of zinc. There were speculations on the significance of this rather unprecedented element, but no one had a very clear idea about its physiological importance. Zinc salts were known to be toxic to plants in small amounts. Therefore there was a great deal of interest taken in their effects, especially in the vicinity of industries which liberated fairly large amounts of zinc into the atmosphere or into the drainage water.

The work of RAULIN, already mentioned, gave definite evidence that zinc in very small amounts is useful for the growth of plants, showing (1869) that zinc, as well as certain other micro-elements, was beneficial to the growth of *Aspergillus* in conjunction with the other necessary mineral nutrients. JAVILLIER published in 1908 the results of his study of the zinc content of about 45 species representing 27 families of plants in which zinc was commonly present. He believed that zinc had an important physiological function, but he was not very clear about its nature. When zinc was added to cultures in which *Aspergillus* was grown, there was a definite increase in the dry weight of the fungus. He found that with increasing amounts of zinc (from one part per 10,000,000 to one part per 10,000), there was an increase in the respiration of sugar in the culture solution, accompanied by an increase in the amount of mycelium produced.

The effects of zinc on the growth of green plants began to be studied about 1913, when VOELCKER published results of pot experiments to test the influence of zinc salts on the growth of cereals. He showed that the addition of zinc up to .01 per cent will have, on the whole, a stimulating result and produce better tillering, but that above that amount it was toxic. MAZÉ published (1914) an important paper showing the beneficial effects of zinc on the growth of maize, concluding that it has a specific effect on the growth of higher plants. In low concentration it seemed to act as a food for the cell, and its physiological action appeared to be linked with sulfur translocation. However, zinc, when present in soluble form, was definitely toxic, even at a very high dilution. For example, zinc nitrate at a concentration of 25 parts per million inhibited the growth of corn roots and killed the plant within one month, although under these conditions the amount of zinc was not sufficient to meet the zinc requirements of the plant. The results of these earlier investigations on the growth of plants supported the conclusion that zinc is a nutrient rather than a stimulant. BERTRAND and his colleagues found small quantities of zinc in the juicy part of citrus fruits, but found larger amounts in chlorophyll-bearing organs. They also showed that the green leaves of various salad plants were richer in zinc than etiolated leaves and assumed that zinc plays a role in chlorophyll production, or at least in some process in which chlorophyll is involved.

In 1926 SOMMER and LIPMAN gave additional evidence of the indispensable nature of zinc for the growth of higher plants. Miss SOMMER later confirmed the results and extended the observations to include a number of other plants. The study of zinc in relation to many agricultural and horticultural problems has been intensively prosecuted. HOAGLAND and CHANDLER discovered (1931 and 1932) that the tree abnormalities in certain areas of

California were due to the deficiency of zinc in the soil, and that when properly supplied, the fruit trees and certain small plants regained vigor, showed improved growth, and produced satisfactory crops of fruit. In 1931 and 1932 four different groups of workers in America discovered independently that treatment with zinc, through the soil or in other ways, will cure a serious orchard disease — one that affects trees of some kinds in some areas and of all kinds in certain areas from Florida westward through Texas, Arizona and California, and northward at least to the Canadian line. This disease went by various names, depending somewhat on the variety of tree which was being studied. On the pecan and the apple it is called "rosette"; on the citrus tree, "mottle leaf"; on the walnut, "yellows"; on the grapevine, stone fruits and some other trees, "little leaf"; in maize it is called "white bud" (Fig. 35).

In 1935 REED and DUFRÉNOY showed the importance of zinc in cell physiology of the orange leaf, and determined its distribution in affected and healthy leaves by micro-incineration. They showed that profound changes in cytological conditions were associated with the recovery of affected leaves after having been sprayed with a solution of zinc sulfate plus lime. Cells which had been practically devoid of chloroplastids had developed an abundance of new plastids which had a marked ability to form starch. ZALESKI and REINHART, in a paper published in 1909 were perhaps the first to point out that zinc sulfate stimulated the respiration of plants (lupine, maize and pea seedlings), and SILBERBERG also showed (1909) that zinc increased the respiration of storage tissues such as beets, sweet potatoes, and kohlrabi. REED and DUFRÉNOY found that the cells of zinc-deficient leaves did not appear to utilize the carbohydrates in respiration. Instead of forming soluble carbohydrates which were easily utilized in respiration, there was a tendency to produce lipoid and phenolic materials, which were obviously of small use to the plant cell. They advanced the theory that zinc has much to do with the activity of sulfhydryl compounds in regulating the oxidation reduction potential within the cells. SCHARRER and SCHROPP made an extensive study on the influence of zinc and cadmium upon plant growth, finding that zinc had a distinctly beneficial effect, except for oats. They were apparently interested chiefly in determining toxic concentrations for the different plants. They concluded that cadmium is more toxic and less stimulating than zinc.

STEINBERG demonstrated (1936 and 1939) that zinc is essential for the growth and sporulation of *Aspergillus niger* and that it seems to be necessary for the utilization of carbohydrates. SKOOG elucidated (1940) the relation of zinc to growth when he showed that the growth hormone (auxin) was scanty in terminal buds and stems of zinc-deficient plants. He concluded that in the absence of zinc there may be an excessive destruction of auxin (probably by oxidation) resulting in restricted growth and development. Zinc seemed to be necessary for the maintenance rather than the synthesis of auxin.

Selenium:- Selenium is present in certain soils of arid regions and certain salts of selenium are used as insecticides. As much as 3,000 parts per million of dry matter occur in some plants of

western North America. Plants absorb relatively large amounts without visible injury and yet they may be fatal to animals which eat them. The toxicity of seleniferous plants was probably first observed by MARCO POLO, who said, in speaking of the Tanguatan Mountains: "Travelers, however, dare not visit these mountains with any cattle but those of the country, for a certain plant grows there which is so poisonous that cattle which eat it lose their hoofs. The cattle of the country know it and eschew it." BRETSCHNEIDER thinks that the poisonous plant was *Stipa inebrians,* described by HANCE in the *Journal of Botany,* 1876, p. 211, from specimens sent HANCE by Belgian missionaries from the Alaschan Mountains west of the Yellow River (*History of European Botanical Discoveries in China,* 1898, London).

Seleniferous soils are found principally in arid and semiarid regions. In 1856 MADISON, an army surgeon stationed at Fort Randall in South Dakota, had his attention called to the illness and death of a large number of cavalry mounts at that station which had grazed upon the luxurious vegetation. The relation of stock poisoning to selenium was later established by FRANKE, of the South Dakota Agricultural Experiment Station, and was followed by a great development of research on the relation between plants and selenium.

The quantity of selenium absorbed from the soil appears to vary with the character of the soil and with the other materials available for plant growth. To a still greater extent, the variability of selenium in plants is due to the selective absorption. BEATH found (1937) one species of vetch (*Astragalus missouriensis*) which had 3 parts per million, but another species (*Astragalus bisulcatus*) had 1250 parts per million, though both species grew on the same small plot of soil. In an adjacent plot, a composite sample of young wheat plants showed a content of 45 parts of selenium, while *Astragalus bisulcatus* growing among this wheat contained 1110 parts per million.

Molybdenum:- The necessity of molybdenum for plant growth was for a time uncertain because of the small amounts required. BORTELS found (1930) that both molybdenum and vanadium promoted growth and nitrogen fixation of *Azotobacter* and he assumed that they acted as catalysers. Subsequently the importance of molybdenum was investigated and fully confirmed by others. STEINBERG extended the work (1936) showing that this element is also necessary for the growth and development of *Aspergillus* and important in nitrogen metabolism. Miss WARRINGTON, who studied the effects of supra-optimal concentrations of molybdenum on plants, demonstrated (1937) that the element was absorbed and formed definite compounds with tannin and with anthocyanin in the plant cell. The essential nature of molybdenum for barley was demonstrated (1937) by ARNON and subsequently established (1939) for tomatoes by ARNON and STOUT. They found that the development of deficiency symptoms was prevented by the addition of the element in a concentration of 1 : 100,000,000 in the culture solution.

The historical discussion of the role of micro-elements in plant nutrition might be extended to include vanadium, titanium, silicon, iodine, chlorine and others, but space forbids. Yet if the

foregoing discussion establishes the validity of the extension of investigations into this new field, it has been profitable.

This brief discussion, incomplete in many respects, shows that the acquisition of mineral nutrients is an intricate, yet highly important phenomenon. The historian of the plant sciences is confronted by the problem of discussing many aspects of this subject which, as yet, seem to be loosely connected with the accepted body of data. The problems of soil formation, of productivity and infertility have been variously studied by geologists and chemists. Absorption and fate of the mineral constituents have been considered by physiologists, at first through ash analysis, then by controlled experiments. Problems of a biophysical nature are still awaiting solution. None of the mineral elements furnishes energy to the plant; they seem to act as catalysts.

Where so many border-line problems await investigation it is difficult to obtain a perspective which allows the historian to make a satisfactory account of the whole subject of the development of the field of mineral nutrition.

Many problems of major importance have not yet been attacked. We cannot rest content until we know the relation of the mineral nutrition of plants to longevity, fruitfulness, resistance to pathological organisms, resistance to water loss, production of alkaloids, phenolic compounds, vitamins, sugars and a multitude of other things. The importance of these things to agriculture cannot be overestimated.

REFERENCES:-

BIRNER, H. und LUCANUS (1866): Wasserkulturversuche mit Hafer. Landw. Versuchsst. 8:128-177.

BRENCHLEY, W. E. (1927): Inorganic plant stimulants and poisons. Longmans, Green, London.

BURD, J. S. (1919): Rate of absorption of soil constituents at successive stages of plant growth. Jour. Agr. Res. 18:51-72.

CHANDLER, W. H. (1937): Zinc as a nutrient for plants. Bot. Gaz. 98:625-646.

CZAPEK, F. (1920): Biochemie der Pflanzen, Bd. 2. 2. Aufl., Fischer, Jena.

LOEW, O. (1903): The physiological role of mineral nutrients in plants. U. S. Dept. of Agr. Bur. of Plant Industry, Bull. 45.

MAZÉ, P. (1936): The rôle of special elements (boron, copper, zinc, manganese, etc.) in plant nutrition. Annual Rev. Biochem. 5:525-538.

MILLER, E. C. (1938): Plant physiology. Ed. 2 (with bibliography). McGraw-Hill, New York and London.

RAULIN, J. (1870): Etudes chimiques sur la végétation. Masson, Paris.

REED, H. S. (1907): The value of certain nutritive elements to the plant cell. Annals of Bot. 21:501-543.

RUSSELL, E. J. (1937): Soil conditions and plant growth. Ed. 7, Longmans, Green, London and New York.

SCHIMPER, A. F. W. (1888): Über Kalkoxalatbildung in den Laubblättern. Bot. Zeit. 46:65, 81, 97, 113, 129, 145.

Chapter XVIII.

HISTORY OF MYCOLOGY.

Early works on fungi:- Most of the early descriptions of fungi were included in general works on plants, and they generally received scant attention. Without adequate knowledge of the microscopic structures, the early botanists attempted to find too many analogies between fungi and flowering plants. By some the fungi were regarded as aborted fetuses of plants.

STERBEECK, who described edible and poisonous fungi, published "Theatrum fungorum" (Antwerp, 1675) and was followed by DILLENIUS who laid the foundations for a classification of the cryptogams (1719). PIER'ANTONIO MICHELI (1679-1737) clarified and extended the knowledge of fungi in his "Nova plantarum genera" (Florence, 1729), which may be taken as a definite starting point in the development of mycology.

The German botanist, J. G. GLEDITSCH (1714-1786), attempted to classify fungi and very logically chose as a basis the organs of fructification. His "Methodus Fungorum" (1753) contained descriptions of 11 genera, which he grouped as follows:

I. Spore-bearing surface exposed

Byssus, Clavaria, Elvela, Phallus, Boletus, Agaricus.

II. Spore-bearing surface enclosed

Peziza, Clathrus, Stemonitis, Lycoperdon, Mucor.

Although GLEDITSCH's work contained little new material, it was illustrated with five good plates.

FELICE FONTANA (1730-1805), an outstanding Italian scientist, published in 1767 a work on the rust of grains, which, although overlooked for many years, is now recognized as one of the first advances in the understanding of the nature of parasitic fungi and their relations to their host plants. FONTANA was educated at Rovereto, Verona, Parma, and at the Universities of Padua and Bologna. He was appointed professor of philosophy at the University of Pisa by FRANCIS I, grand duke of Tuscany, holding this chair until Archduke LEOPOLD called him to Florence to build the Museum of Physics and Natural History, which even today is one of the principal ornaments of that city. He wrote articles in Italian and French on blood globules, on the circulation of the sap in plants, on the "tremelle of ADANSON", on snake poisons, and also a few articles on plant diseases.

FONTANA's description of the rust of cereals was the first which really recognized the parasitic nature of the fungus which attacks plants. He understood, better than anyone who had preceded him, that the spots on the cereal plants were caused by minute plants which nourished themselves at the expense of the tissues of the host. FONTANA said that the theory held by many of his time concerning the diseases of grains, such as blight and rust, was that they had been caused by solar rays which, united and brought to a sharp focus by the drops of water on the tender small plants,

burnt, scorched, and consumed the grain and leaves. He proceeded to show how inadequate any such theory would be, by spraying water on the most tender living plants and also on the leaves and stalks of already dried and completely withered plants. Subsequently, he exposed them for a very long time to the hottest rays of the sun at midday, and never noticed any burning or blackening in any part. He also placed small lenses and pieces of fused glass on various leaves, and found that the light which had been focused in that way upon them was entirely harmless and inactive.

Summing up the results of his observations on the nature of the rust of cereals, FONTANA concluded by saying that he had observed with the microscope that the rust he gathered from the stalk or leaves with a knife was made up at times only of small eggs, and at other times of "piled nails without any single eggs attached to them". From this he concluded that there must be two kinds of rust or at least two different kinds of spores of the same rust. This led him to the discovery of the urediniospores and the teliospores. He was, of course, mistaken about many things that he saw, but he never mistook the real nature of the infecting organisms, and recognized that the small bodies which he saw with the microscope were the fruits or pericarps of the rust plant. Concerning the nature of these small microscopic plants which live on the grains, he said, "First of all, if the stalk and the leaves are attacked by this terrible malady, the best set of kernels promising a heavy yield is reduced to nothing, or almost nothing, because such a great number of greedy and gluttonous plants absorb nearly all the nutritive humor of the grain, causing it to become wasted and consumed because of the loss of the nourishing chyle". It was nearly fifty years before anyone else wrote anything which showed such good sense in relation to fungi and their host plants.

So enthusiastic was he about the importance of his work, and so anxious that others should participate in the pursuit of his study, that he went on to say:

> "the talents of many learned botanists could be used to greater advantage in the little-known field of the vegetable kingdom. If, instead of seriously pursuing new systems and enriching with new barbarous words one of the most delightful, and perhaps the most useful, branches of the science of nature, they observed the structure of plants more closely by examining their nature and economy more in detail, especially in the case of the so-called imperfect plants, which can be properly observed only with the microscope and concerning which confusion, uncertainty, and obscurity reign, even after MICHELI and DILLENIO". (translation by PIRONE).

The scientific period initiated:- The opening years of the 19th century witnessed a great clarification of ideas concerning algae and fungi. Many observers who had seen the filamentous hyphae of fungi in the tissues of the host plants had mistakenly regarded them as strands of congealed sap, others had regarded the spore pustules as morbid symptoms caused primarily by weather or soil conditions. Mystical and erroneous beliefs about fungi gradually were discarded and men began to study their actual characters and relations. We may infer that, although this new movement owed its inception in part to an increasing interest in microscopy, it was perhaps more directly due to the great advances in botany in

the preceding century. Botany had become a science by this time, because knowledge about plants had increased and because rational ideas had been formulated. It is true that there were still many imperfections and much remained to be done, but the way had been found.

There was first a period of accumulation of knowledge and, almost simultaneously, a logical classification of fungi.

In 1801 CHRISTIAAN HENDRIK PERSOON (1762-1836) published the first reliable systematic account of the fungi, the "Synopsis Methodica Fungorum". It was the solid foundation on which others were to build.

PERSOON's meritorious work stands in such contrast to the pathos of his life that a few words about his career are appropriate. He was born at the Cape of Good Hope, at that time a colony of Holland. His father seems to have been a man of property who sent his son, when 12 years old, to Europe to study where young PERSOON appears to have worked industriously and to have gained the affection of his teachers. About 1800 he took up his abode in Paris whither his reputation had preceded him and where he was favorably received. It has been reported that he was eventually forced to live in straitened circumstances. Nevertheless from his dingy garret lodgings PERSOON corresponded with eminent scientists and issued copy for books of fundamental importance in botany.

In 1818 he published a book on the edible and poisonous mushrooms, and from 1822 to 1828 an incomplete work, the "Mycologia Europaea". In 1805 his two volume work, the "Synopsis Plantarum" appeared which contained a comprehensive enumeration of the flowering plants then known.

Reverting to his work on the classification of fungi it is interesting to see how simply and perfectly he adapted the binomial system of nomenclature to the chaotic group which most botanists had shunned. He erected two large classes, each of which contained three orders.

CLASSIS PRIMA: ANGIOCARPI

Ordo Primus:	Sclerocarpi (*Sphaeria, Hysterium,* etc.)
Ordo Secundus:	Sarcocarpi (*Sphaerobolus, Sclerotium,* etc.)
Ordo Tertius:	Dermatocarpi
	Tricospermi (*Geastrum, Lycoperdon,* etc.)
	Gymnospermi (*Mucor, Uredo, Puccinia,* etc.)
	Sarcospermi (*Cyathus*)

CLASSIS SECUNDA: GYMNOCARPI

Ordo Quartus:	Lytothecii (*Clathrus, Phallus*)
Ordo Quintus:	Hymenothecii
	Agaricoidei (*Amanita, Agaricus,* etc.)
	Boletoidei (*Daedalea, Boletus*)
	Hydnoidei (*Hydnum,* etc.)
	Gymnodermata (*Thelephora, Merisma*)
	Clavaeformes (*Clavaria, Geoglossum*)
	Helvelloidei (*Helvella, Tremella,* etc.)
Ordo Sextus:	Naematothecii (*Monilia, Isaria,* etc.)

He began the science of mycology with practically nothing, and created a system. He abandoned vague classes, such as *Byssus*, and established genera and species according to the system of bi-

nomial nomenclature already adopted for other plants. He first recognized rust fungi as a distinct group in 1818, saying "A small but very natural family, very rich in species is that of the Uredineae, all parasitic, mostly under the epidermis of green leaves".

The scientific classification of the fungi was carried on by ELIAS FRIES (1794-1878), son of a prominent, well-educated minister of the established church of Sweden, who instructed him in natural history studies and gave him an exceptionally fine training in the Latin language. While still a child he found a specimen of *Hydnum corraloides* which turned his attention to the study of fungi.

FRIES devoted his principal attention to the Hymenomycetes, having apparently a poor opinion of parasitic fungi and an antiquated idea of their nature. He was first at Lund, then in 1834 went to Upsala where he had opportunities to know practically all the agarics that grew in Sweden. When he began, PERSOON had almost finished his work, and it was the foundation on which FRIES built. His system of classification, which is a slight modification of PERSOON's, has lasted to the present, and is characterized by the accuracy and conciseness of description as well as by its usefulness. "Systema Mycologicum" (1821-1829) gave a compendium of all genera and species known at the time. His monograph on the *Hymenomycetes* of Sweden was published 1857-1863. His crowning achievement in mycology was a complete text on the *Hymenomycetes* of Europe, which included, not only a complete account of his own observations, but a synopsis of the literature on the subject, and was finished on his eightieth birthday, the "Icones Selectae Hymenomycetum".

The soundness of the early work is witnessed every day and was recognized by the International Congress which drew up rules for nomenclature of the fungi in 1910 at its meeting in Brussels. It was agreed then that FRIES' "Systema Mycologicum" should be the starting point for the nomenclature of the fungi, except for the *Uredinales, Ustilaginales,* and *Gasteromycetes* which should date from PERSOON's "Synopsis Methodica Fungorum".

FRIES is also regarded as the founder of the system of classifying lichens, based on the characters of the organs of fructification, which was elaborated in his "Lichenographia Europaea Reformata" (1832). It was he who distinguished between gymno- and angiocarpous lichens.

The illustrious French mycologist LÉVEILLÉ (1796-1870) published in 1837 a paper of importance in which he divided the fungi into two large groups — the basidiospores (Basidiomycetes) and thecaspores (Ascomycetes) based on the character of the spore bearing apparatus. It was his work and that of BERKELEY which gave exact information concerning the basidia in the *Hymenomycetes* and led to their subsequent study.

Systematic works:- The value of microscopical characters as a basis for the classification of fungi was demonstrated by A. C. J. CORDA (1809-1849), a Czechoslovakian, who was custodian of the National Museum in Prague (appointed in 1835). His six volumes of drawings of the microscopic features of fungi were the first extensive series ever made, albeit they often are inaccurate, due either to his lack of care or to imperfections in his microscope.

He included many besides the fleshy fungi which FRIES had described. CORDA was the first to observe (1839) the penetration of the germ tube of a fungus through the stoma of leaf, and also established the fact that the submerged mycelium is a part of the fungus, not some other organism. In 1849 when returning from a collecting trip to Texas, the ship on which he travelled and all passengers were lost in a storm in the Gulf of Mexico, and his collections were lost with the ship. ANDERS SANDÖE ÖRSTED (1816-1872) made a journey to Central America where he found a number of new fungi which were sent to FRIES and described by him.

The eminent British mycologist, MILES J. BERKELEY (1803-1889) contributed "Introduction to Cryptogamic Botany" (1857) which was regarded for many years as a standard work on the subject and useful to all mycologists. It was followed (1860) by his "Outlines of British Fungology", a work which described all species then known in the British Isles. BERKELEY's pertinent discussions of subjects such as the habitats, variations, and the geographical distribution of fungi testify to his ability to visualize the biological importance of fungi in the organic world. COOKE's "Handbook of British Fungi" (1871), and PLOWRIGHT's "British Uredineae and Ustilagineae" (1889) also contain important materials.

The science of mycology was initiated in North America by LOUIS DAVID VON SCHWEINITZ (1780-1834), a Moravian pastor who worked at Bethlehem, Pennsylvania and at Salem, North Carolina. His work in the field of mycology entitled "Synopsis Fungorum in America Boreali Media Digentium" was published in 1834. SCHWEINITZ' large herbarium was bequeathed to the Academy of Natural Sciences of Philadelphia. The fungus flora of the southeastern United States was later studied by Rev. M. A. CURTIS (1808-1872) and by H. W. RAVENEL (1814-1887), for whom the genus *Ravenelia* of the *Uredinales* was named. RAVENEL's extensive collections were sold after his death to the British Museum.

C. H. PECK (1833-1917) was one of the eminent mycologists of the United States, describing and publishing many theretofore unknown fungi. From 1867 to 1915 he was botanist for the New York State Museum at Albany, when he issued "Reports on Botany" which contain a wealth of information concerning native species of fungi.

J. B. ELLIS and B. M. EVERHART studied North American fungi. Their well-known work on the *Pyrenomycetes* was published in 1892. R. THAXTER's elaborate monograph on the *Laboulbeniaceae,* E. A. BURT's work on the *Thelephoraceae,* and many other studies on special groups are worthy of more extensive mention than can be here devoted to them.

J. C. ARTHUR (*b.* 1850) has been an assiduous student of the *Uredinales,* especially the connection between their aecial and telial stages, utilizing the methods of cultures to determine the alternate hosts. He was professor at Purdue University from 1888 to his retirement in 1915. His work "The plant rusts" (1929) is the most complete treatise on the subject published in the United States.

DE BARY, of whom more will be said in a subsequent paragraph, thoroughly imbued with a belief in natural descent of organisms, attempted to emphasize relationship in his classification of fungi

published in "Vergleichende Morphologie und Biologie der Pilze u.s.w." (1884). His arrangement was:

I. Series of the Ascomycetes

1. Peronosporeae (with *Ancylisteae* and *Monoblepharis*).
2. Saprolegnieae.
3. Mucorini, or Zygomycetes.
4. Entomophthoreae.
5. Ascomycetes.
6. Uredineae.

II. Groups which diverge from the series of the Ascomycetes or are of doubtful position

7. Chytridieae.
8. Protomyces and Ustilagineae.
9. Doubtful Ascomycetes (*Saccharomyces*, etc.).
10. Basidiomycetes.

Groups 1-4 were designated *Phycomycetes* on account of their close approximation to the algae; groups 7 and 8 in the second category could be considered with the *Phycomycetes;* group 9 naturally in connection with 5, 10 and 6. DE BARY like other mycologists found difficulty in classifying the *Saccharomycetes.* He was confident that they were related to the *Ascomycetes* but was uncertain whether the resemblances were the expression of natural and phylogenetic affinities. The final evidence on this question was afforded by GUILLIERMOND (in 1903, 1905, and 1917) when he discovered sexual fusions which result in the formation of asci.

GÄUMANN's recent classification in his "Vergleichende Morphologie der Pilze" shows the simplified modern idea.

1. Flagellatae
2. Myxomycetes
3. Archimycetes
4. Phycomycetes
5. Ascomycetes
6. Basidiomycetes

The continually growing body of knowledge of fungi began about the middle of the 19th century to be augmented by an elucidation of the hitherto unknown life histories of these organisms. The confused ideas about the nature of fungi then began to be dispelled by exact observation and experimental work.

Polymorphism and parasitism:- The process of unification and simplification of knowledge of the fungi gathered momentum from the discovery of polymorphism in fungi by the brothers TULASNE, and of heteroecism in the *Uredineae* by DE BARY. Their predecessors gave only the description and configuration of the external forms of fungi, emphasizing the shape and size of the spores, finding that, in a general way, the distinct form of the reproductive organs was sufficient for determining, not only genera, but species. They naturally concluded that distinct spore forms represented distinct species, as indeed they generally do, but TULASNE discovered that certain fungi may have different spore forms in different stages of their life histories.

LOUIS-RENÉ TULASNE (1815-1885) and his brother CHARLES intimately coöperated in a life-long study of botany. LOUIS was appointed assistant naturalist in the Museum of Natural History

in 1842, one year after he had published his first scientific paper. When this appointment was made, CHARLES relinquished his medical career and all thought of an independent position in the world. He was an artist of unusual dexterity who introduced a new type of botanical illustration, which, though often imitated, has never been excelled.

Their *magnum opus* was the "Selecta Fungorum Carpologia" in three magnificent quarto volumes published in 1861-1865, in which they demonstrated the pleomorphism of ascomycetes which had been denied by some contemporary mycologists. They depicted for the first time the conidia, perithecia, and asci of many important parasitic ascomycetes. In addition to his accurate descriptive work TULASNE concerned himself with the place of fungi in the biological realm, giving one of the best accounts of their role in the cycle of nature. He emphasized the phenomena of disintegration and decomposition in which fungi coöperate with physical and chemical agencies to convert the dead bodies of plants and animals into materials which may be utilized again by successive generations.

> " . . . innumerable cohorts of Fungi supply these intermediate forms for the breaking up of the vegetable or animal dust, and in them it takes on a new life and is raised by degrees to a higher standing. This is indeed the reason why, as soon as any vegetable whatever, herb, shrub, tree, or even the smallest part thereof, is dead, it at once becomes the prey of Fungi, legions of which come in succession one after another, and grow and multiply the more luxuriantly, the quicker the host diminishes and is consumed by decay, until nearly the whole of it is exhausted by them, and converted into humus from which afterwards there will be born a progeny of higher species . . . "
>
> " . . . But if anyone wonders at the innumerable forms of Fungi and in his narrow and petty mind thinks them superfluous, let him contemplate the whole theatre of nature and then he will admire, throughout each and every rank of animals and vegetables, a similar abundance of types and a not less prodigious diversity of forms derived from the same prototype."

TULASNE in investigating the ontogeny of fungi discovered many important facts about the germination of spores and the evolution of mycelium from germ tubes (Fig. 36). Sclerotia and rhizomorphs were faithfully described. He published in 1852 a memoir on lichens in which he announced that the thalli contain filaments remarkably like those of fungus hyphae, adding the pertinent declaration that he had observed remote analogies between their reproductive organs and those of certain fungi. This seems to have opened the way for the discovery of the true nature of lichens, and was another advance in the unification and simplification of mycology. In addition to his mycological work, TULASNE studied the problem of the fertilization and embryology of phanerogams, correcting the erroneous idea that the development of the embryo occurs in the tip of the pollen tube. From 1843 to 1855 he published on the taxonomy of phanerogams, chiefly South American forms.

PRINGSHEIM in 1857 contributed the first incontrovertible evidence of sexuality in the fungi when he discovered the process of fertilization in *Saprolegnia*. Further developments of the knowledge of fertilization have been given in chapter XI of this book.

The first well-founded exposition of the heterotrophic nature of the fungi, especially of the parasitic fungi, came from DE BARY in 1853 in his "Untersuchungen über die Brandpilze und die durch

sie verursachten Krankheiten der Pflanzen", who then gathered up the few grains of truth found by his predecessors and combined them with his own epochal discoveries of the life cycles of several very important fungi.

Before discussing the nature of his work some facts concerning the man must be presented. ANTON DE BARY (1831-1888) was the son of a physician at Frankfurt-on-the-Main. He studied at Heidelberg, Marburg, and Berlin. After practicing medicine for only two months he accepted a position as docent at Tübingen, then he went to the Hochschule at Freiburg, where he established the first botanical laboratory in Germany. While there he wrote the book which revolutionized all ideas on the fungi, namely "Morphologie und Physiologie der Pilze, Flechten, und Myxomyceten" (1864-66). In 1866, refusing a call to Leipzig, DE BARY accepted the offered chair of botany at Halle, where he remained for six years, whence he went to the newly organized university in Strassburg in 1872 and built up a splendid botanical institute where he remained until death claimed him in 1888. Students from Germany and other countries gathered there to work under his inspiring leadership. It was also a productive time for DE BARY when, in addition to scientific papers, he wrote his two memorable books, "Vergleichende Anatomie der Vegetativen Organe der Phanerogamen und Farne" (1877) and "Morphologie und Biologie der Pilze, Mycetozoa, und Bacterien" (1884).

Today we take for granted that parasitic fungi are causes of disease of the host, but in 1853 it was otherwise. DE BARY produced evidence that the "congealed sap" out of which the *Uredinales* and *Ustilaginales* arise is in reality mycelium and is not different from the fungus hyphae growing from the spore. He showed that *Phytophthora* can penetrate the host through the stomata, though other fungi may penetrate the epidermis. Even different spore forms of a species may not behave similarly. A further question was the choice of a host; certain species like *Phytophthora omnivora* could attack almost every plant, others only a single, or a few related species, or related genera.

Heterocism in the rusts was first definitely established by DE BARY in 1864 and by ÖRSTED at approximately the same time; though farmers for at least a century rightly maintained in opposition to botanists that cereals grown in the vicinity of barberry shrubs were particularly subject to attacks of *Puccinia*. DE BARY originated the method of employing controlled cultures for securing exact knowledge of polymorphism, parasitism, and general life histories.

Parasitism and saprophytism were terms without meaning until DE BARY defined them. He was a physiological mycologist, classifying fungi according to their nutritive adaptation into (1) Pure saprophytes, (2) Facultative parasites, and (3) Obligate parasites. He ascertained how the fungus attacks the host, showing that in many cases spore germination occurs only in the presence of the host. He showed that many fungi live epiphytically on the host, sending to it only haustoria, while others live endophytically in intercellular spaces or even in the cells themselves. Many remain strictly localized, others grow through the entire host. DE BARY discovered (1886) the enzyme cytase which destroys cell wall, and isolated it from the fungus *Sclerotinia* which he was

investigating. He demonstrated that its activity was destroyed by heating it even for a very short time.

It must be noted that DE BARY, although conscious of his illuminating discoveries, never regarded the problems as finally solved. On the contrary, he generally concluded by saying that later investigation will doubtless bring to light additional important facts.

An important addition to our knowledge of parasitic organisms was provided by the work of M. S. WORONIN (1838-1903) on the clubroot of cabbage caused by *Plasmodiophora*, a myxomycete. On account of the wealth and the position of his parents, young WORONIN received a liberal education, and having graduated from the University of St. Petersburg went to Heidelberg and thence to Freiburg, where he came under the influence of ANTON DE BARY. In 1869 and 1870 he gave lectures on fungi in the University of St. Petersburg, and from 1873 to 1875 was Reader of Mycology and Anatomy of the Plant Cell in the Higher Medical School for Women at St. Petersburg. He refused higher appointments than these, preferring to live and employ his means in the way in which he felt he could serve his fellow men best.

When WORONIN went back to Russia, he soon began investigations on the clubroot of cabbage, which was a serious drawback to the cultivation of that plant in the vicinity of St. Petersburg. The disease is known, needless to say, in many other countries: England, Scotland, Belgium, France, Germany, Spain and North America. WORONIN undertook the investigation of the cabbage clubroot independently in 1873 and completed it in the autumn of 1876, discovering that the actual cause of the disease was a new organism, *Plasmodiophora brassicae*. He said nothing about the novelty of the discovery, but we may pause to comment that this was the first time that parasitism had been demonstrated in the *Myxomycetes*, and great credit should go to the man who had the insight into the nature of fungi which would warrant him to undertake the investigation of a disease caused by one of these very primitive organisms.

Experimental work in mycology was expedited by the improvements in technique introduced by DE BARY, BREFELD, and VAN TIEGHEM. BREFELD added gelatin or agar to liquid media, thereby getting a moist surface on which the organisms could be cultivated. VAN TIEGHEM introduced the small glass cells which today bear his name, in which it is possible to observe the development of microörganisms under sterile conditions. Mycology adopted, also, the new techniques evolved by PASTEUR and KOCH.

DANGEARD and SAPPIN-TROUFFY in 1893 discovered the sexual fusion of nuclei in the teliospore, following which there is a true reduction of the number of chromosomes preceding the development of the promycelium. Subsequently DANGEARD discovered a similar phenomenon of nuclear fusion (karyogamy) in *Ustilagineae* then in *Ascomycetes* and *Basidiomycetes*. BLACKMAN (1904) and CHRISTMAN (1907) demonstrated that there was a true alternation of generations in the *Uredineae*.

REESS started (1870) fundamental studies in the classification of yeasts, which were supplemented by HANSEN's epoch-making work in 1879. REESS distinguished species according to the appearance of the cells, calling the ellipsoidal cells *Saccharomyces ellipsoideus*, and the sausage shaped yeasts *S. Pastorianus*, etc. HAN-

SEN showed, however, that one and the same species of yeast can occur in all these different forms, and that, as a consequence, the species cannot be determined in that way. EMIL HANSEN (1842-1909) originated a technique for pure culture of yeasts and inaugurated a new era in the biology of the fungi of alcoholic fermentation. From 1877 to the end of his life he was head of the physiological department of the Carlsberg Institute in Denmark.

The physiological action of some of the fungi has been extensively investigated on account of their enzyme production. Indeed, the biochemical activities of certain fungi occupy the attention of important institutes for research. Yeast, though observed by LEEUWENHOEK, was discovered and scientifically described almost simultaneously by CAGNIARD-LATOUR (1777-1859) a French engineer and physicist, and by THEODORE SCHWANN (1810-1882), well known as a co-founder of the cell doctrine. CAGNIARD-LATOUR stated that yeast is organized matter and that probably the formation of carbon dioxide and of alcohol is caused in some way by its growth. SCHWANN refuted the idea which originated with GAY-LUSSAC, *viz.*, that oxygen was the immediate cause which induced alcoholic fermentation, by showing that oxygen did not promote oxidation if the air in the flask had been previously strongly heated. Furthermore, the introduction of fresh quantities of air which had been heated previously did not promote fermentation.

Physiologic races and heterothallism:- DE BARY clearly showed that parasitic fungi are generally restricted in the range of their hosts. Since his day others have followed up the question of specialization, finding that there are groups within a species which differ in their host specialization. SCHROETER was the first to observe (1879) that there are distinct physiologic races of parasitic fungi and ERIKSSON demonstrated (1894) that physiologic races of rust fungi may not differ morphologically. SALMON further demonstrated (1903) that physiologic races exist among the powdery mildews. It has since been learned that physiologic specialization is very common among widely separated groups of fungi.

The differences between races are distinguished in part by their morphology but principally by their physiological behavior. STAKMAN is positive that one may distinguish between physiologic races on the basis of cultural characters on artificial media, or in the case of some parasites, like *Puccinia graminis,* use of the host plant as the culture medium in growing the fungus. This has led to the distinction of more than 50 physiologic races of *Puccinia graminis tritici.*

H. M. WARD, in 1903, launched the concept of "bridging hosts". He reported that rust from species A could not infect species C, but it might infect species B, intermediate taxonomically between A and C. On species B the rust acquired the ability to infect C; therefore, it seems as though species B was a bridge between A and C. This theory of adaptation and bridging hosts was for a time quite widely accepted, but later investigations indicate that physiologic races, at least, do not gradually adapt themselves to new hosts. Neither has it been possible in later years to substantiate the results of earlier investigators on bridging hosts. A number of examples of apparent "bridging", when analysed, have been

proved to be due to mixed cultures. The work of STAKMAN, PARKER, and PIEMEISEL, indicates that physiologic races, at least in the rust fungi, do not change pathogenicity as a result of host influences.

It has been variously assumed that new physiologic races may arise in one of four ways: Adaptation, hybridization, heterocaryosis, or mutation. Most of the evidence at present seems to indicate that physiologic characters in pathogenic fungi are, at least, as stable as morphologic characters. They are due to genetic factors, the expression of which may be influenced to a considerable extent by environment, but there is not strong evidence that they can be changed by environment.

The so-called "somatic mutations" or "saltations" are being more and more observed, especially in the fungi. These somatic changes may be merely expressions of fluctuating variability, of a special kind, to be sure, but apparently brought about and reversed through the influence, it may be, of the internal environment. What the nature of these influences may be, which cause a temporary "constancy", we do not yet understand. Through how many generations such an apparent constancy must be taken to establish its stability is certainly a vexing question. The psychology of the investigator, his temperament, and his established viewpoint influence the interpretations drawn from such experiments.

The mutation of pathogenic fungi is interesting enough as a biological phenomena, but the vital question for the mycologist is: "Is there a change in appearance?" Sometimes there is. CHRISTENSEN found that some mutants of *Helminthosporium sativum* behaved like their parents, others were less virulent, and still others were much more virulent than their parents. It has been known for a long time that *Rhizoctonia solani* has a very wide host range, but it has been learned only recently that it includes many races having distinct differences with respect to their pathogenicity. It has been observed more than once that a variety of crop plants may apparently suddenly lose its resistance to a parasite. The phenomenon may be explained now by assuming that another physiologic race (possibly a mutant) of the fungus suddenly appeared. WATERHOUSE has also shown (1929) that new forms may arise by hybridization.

BLAKESLEE discovered (1904) heterothallism in some of the *Mucorineae* which he could distinguish by their copulative power. These strains he designated as "plus" and "minus". Hyphae of the same strain do not unite to form zygospores; hyphae of different strains, on the contrary, unite to form fertile zygospores. DODGE described (1920) heterothallism in *Ascobolus magnificus* and BETTS described (1926) this phenomenon in *A. carbonarius* and showed that half of the spores in the ascus are of one sex and half of the other, indicating that there is a segregation of sex factors during the divisions which occur during ascus formation. SHEAR and DODGE who investigated the fungi of the *Monilia sitophila* group found (1927) that, instead of one, there are at least four species which had been included under that name. Furthermore, two of the species are heterothallic. Cultures from single spores of the heterothallic species produce only conidia, but the mating of reciprocal haplonts produce perithecia. The physiological significance of hormones in heterothallic fungi has been

demonstrated (1939 and 1940) in *Achlya* by RAPER, in the formation of antheridia and oögonia. He found that hormones produced by the hyphae can cause a coördination in the processes of reproduction which appears as a chain of reactions.

The final explanation of the function of the spermatium of the *Uredineae* was afforded (1927, 1931) by CRAIGIE, who cleared up a problem which had long awaited solution. He showed that these fungi may be heterothallic and that both plus and minus strains of mycelia develop from germination of sporidia. He mixed nectar from a minus group of pycnia with pycniospores from a plus mycelium and found that aecia subsequently appeared on the leaf of the host plant. CRAIGIE interpreted this to mean that the pycniospores are unisexual and produce unisexual mycelia, and that aecia are formed by the interaction between pycniospores from mycelia of the opposite strain.

Pasteur's work:- The great historic importance of LOUIS PASTEUR (1822-1895) in science demands mention in this chapter, although he was not *sensu strictu* a mycologist. He showed that fermentation and putrefaction were processes, not of death, as some had said, but of life. The results of his work have contributed to nearly every branch of physical and natural science. Working initially in chemistry he discovered optically active substances and separated them into isomeric compounds having identical chemical, but different physical properties. Thus he became the founder of modern stereo-chemistry. He discovered the fundamental nature of fermentations of living microörganisms and showed that they produce acetic, butyric, and lactic acids. He discovered in 1861 that yeast and several species of bacteria are able to live in the absence of oxygen, and that such life is associated with the phenomena of fermentation. In answer to his critics he demonstrated that processes of putrefaction and fermentation are initiated only by germs which exist in the atmosphere. He promptly applied many of his discoveries to the industrial problems of beer and wine making. His epoch-making works on anthrax and hydrophobia are well-known contributions to animal pathology. KOCH, HANSEN and many others built on the foundation which PASTEUR laid.

Having shown that each infectious disease is caused by a specific organism, he set free the minds of men from an age-long fear of scourges from an invisible foe. The world of today hardly realizes what torments, what gnawing agony, what tragic terrors had their roots in the belief that demons of disease descended spasmodically from nowhere.

PASTEUR's results provoked an explosion of wrath, ridicule, and sarcasm in the German schools of chemistry leading to the oft-mentioned and regrettable controversy with LIEBIG. In the tumult which ensued the opponents lost sight of the fact that they were not fighting for the same thing. LIEBIG contended for a theoretical and PASTEUR for a biological conception; both were more or less right. PASTEUR's ideas were supported by many independent investigations at home and abroad, he, himself, proving that living cells were really necessary for the production of fermentation, and that these living microbes readily gained access to liquids as soon as they were exposed to the air. He also showed that there was

a definite decomposition (autolysis) of the yeast during fermentation and that LIEBIG was, in that particular, essentially correct. Not only did he show that no ammonia was split off during the fermentation, but, on the contrary, ammonium salts could be consumed in the process.

One of the important scientific events of the 19th century was PASTEUR's overthrow of the belief in spontaneous generation of life under ordinary conditions. Challenged as he was by POUCHET, PASTEUR carried out arduous and oft-repeated experiments to prove that the microörganisms of putrefaction and fermentation were not spontaneously generated in a non-living medium. In the end the two antagonists were allowed to perform their experiments before the Académie des Sciences in Paris. PASTEUR's triumph convinced some of the foremost members of the Académie and his results were confirmed by other workers.

Biochemistry:- The industrial importance of yeast has in recent years promoted an ever-growing volume of investigations in its biochemistry. BUCHNER made an important advance when, in 1897, he extracted, from yeast which had been ground and pressed, a zymase which caused alcoholic fermentation. Subsequently the zymase thus extracted proved to be a mixture of at least four enzymes.

In the dispute between LIEBIG and PASTEUR concerning the recognition of the nature of alcoholic fermentation, it signified that neither of them was right, but that, at the time, a third man came nearest to the truth, *viz.*, TRAUBE, who postulated as early as 1858 that all of the fermentations brought about by the living organisms were caused by enzymes secreted by the cells. Finally, when BUCHNER and HAHN discovered cell-free fermentation, it had far-reaching consequences, not only for the industries but for fundamental biological knowledge. BUCHNER had reported in 1899 that he was able to extract zymase from yeast cells by heavy pressure. He determined that the yeast juice obtained in this way induced the fermentation of various monosaccharides and of maltose, and that this capability was not lost either by the action of chloroform, benzene, or sodium arsenate, or by filtration, evaporation, or precipitation with alcohol.

The meritorious work of BUCHNER and HAHN showed the way for the investigation of the sequence of carbohydrate degradation and the enzymology of many important biological systems. By their discovery of cell-free fermentation, they not only settled the dispute between LIEBIG and PASTEUR, but also left to posterity a means and a method for the investigation of the whole question of carbohydrate transformation.

HARDEN and his associates investigated extensively (1906-1911) the biochemistry of alcoholic fermentation discovering, amongst other things, that a salt of hexose phosphoric acid acts as a coenzyme in the fermentation of glucose. The true rôle of phosphates in the metabolism of living yeast cells is, notwithstanding assiduous study, not yet fully known. Although yeast cells may break down carbohydrates by a detour of intermediate phosphorylation, it is by no means certain that it is the only way in which the transformation is accomplished.

Aspergillus oryzae which is used in Japan for the fermentation of sake, an alcoholic beverage, produces a notable amount of dia-

static enzymes. As a result of an extensive study of the enzymes of *A. oryzae* and other fungi, TAKAMINE introduced (1910) into commerce products of high enzymic activity under patents, which are sold under the names of "Takadiastase", "Polyzime", and others.

WEHMER discovered (1893) two species of fungi which produced citric acid when grown upon cane sugar solution, creating for them the genus *Citromyces*. It was eventually found, however, that *Aspergillus niger* produced greater yields of the acid and was of greater practical value. At the present time, the quantity of citric acid being made in England, Belgium, the United States and Japan, is so great that they are virtually independent of the imported acid made from citrus fruits.

Fats are synthesized from carbohydrates by a large number of fungi. Until recently, however, only one species, usually known as *Endomyces vernalis*, was of more than theoretical interest, since it was used for large scale production of fats in Germany toward the end of the first World War. The production of fats by *Penicillium javanicum* has been found to be very large. Under the best conditions, the weight of fat obtained amounts to about 40 per cent of the weight of the mycelium.

One of the best sources of the vitamin B complex is yeast, which is in fact one of the very few readily accessible foods containing all the four or more factors which comprise the vitamin B group. The importance of these factors has led manufacturers to put on the market a number of preparations of high potency made from yeast extract or from autolysed yeast.

Ergosterol is synthesized by a number of moulds as well as by yeast. This substance is the precursor of vitamin D and there are a number of preparations on the market at the present time. Although ascorbic acids (vitamin C) have not yet been obtained as metabolic products of fungi, substances closely related in chemical structure are produced by certain species of *Penicillium*.

NIELSEN was successful in isolating (1930) an auxin, or growth-promoting substance, from the substrata on which either *Rhizopus suinus* or *Absidia racemosa* had grown. The active substance which he designated "rhizopin" is apparently identical with 3-indole acetic acid. Subsequently it was found that other species of fungi may produce this compound which has a pronounced ability to promote plant growth.

Lichens:- The true relationship of lichens to other plants waited some time for elucidation. The final solution was obtained by mycologists, but not without opposition from those who held the prevailing orthodox views of plants. The descriptive work of FRIES has been previously mentioned. TULASNE in 1852 announced that there were filamentous elements in lichens which resembled nothing so much as fungus hyphae, and added that he observed the somewhat remote resemblance between the reproductive organs of lichens and certain fungi. In a few years active work on the problem was undertaken by DE BARY and others with the result that they discovered that there was in the lichen a remarkable association between algae and fungi.

For a time it was assumed that the globular alga cells were the reproductive organs of the lichens, and we must admit that it was a natural assumption in the case of certain gelatinous forms.

SCHWENDENER finally demonstrated (1868) that the alga and fungus lived symbiotically in the lichen thallus, bringing thereby a new concept into the realm of biology. BARANETZKY demonstrated (1867) that the alga could be separated from the lichen and grown separately if conditions were suitable. REESS (1871), BORNET (1873) and STAHL (1877) experimentally produced lichens by combining algae and fungi. STAHL planted spores of *Endocarpon* among green cells or gonidia obtained from the same thallus and he found it to bear both spermagonia and perithecia. BONNIER went a step further by using pure cultures of a fungus and of a unicellular alga and producing synthetically a lichen under aseptic conditions. It was found upon further investigation that the majority of lichen-fungi belong to the ascomycetes, but a few belong to the hymenomycetes. SCHWENDENER found a large number of algae capable of entering into the symbiotic association in a lichen. DE BARY pointed out that the fungus as a strictly obligate parasite is dependent for its vegetative growth on the alga, without which it cannot reach its full development, and in most cases scarcely gets beyond the first stages of germination.

Mycorrhiza:- The remarkable symbiotic association of fungi with the roots of many plants affords a remarkable parallel with the lichen and affords further insight into the nature of biological adaptation. The fungus hyphae in some cases form an enveloping weft of mycelium on the surface of the roots (ectotrophic mycorrhiza), as in the case of beech roots; in other cases the fungus hyphae enter the root and are found in the parenchyma cells (endotrophic mycorrhiza), as in the case of *Andromeda polifolia.*

The real nature of the mycorrhiza was first stated in 1881 by KAMIENSKI, who studied the roots of the non-chlorophylliferous plant, *Monotropa.* He believed that the fungus played an important role in the absorption of food material by roots, since no healthy root-cell was in contact with the soil. He distinguished clearly between parasitism and symbiosis, though he left unanswered many questions about the phenomena of nutrition. FRANK discovered (1885) the fungal associations in green plants and studied the roots of oaks, beech, hornbeam, and conifers. He coined the word mycorrhiza and regarded the association as something of a morphological entity, emphasizing the symbiosis. He assumed that the fungal association contributed to the ability of roots to absorb, not only water and mineral nutrients, but organic compounds derived from the decay of soil organic matter. Endotrophic mycorrhiza of the orchids and heaths were also studied by FRANK and their relations to roots and root-cells discussed. His experiments demonstrated that beech seedlings provided with mycorrhizas and grown in humus lived longer and were thriftier than seedlings in sand or water cultures containing the necessary nutrients in the form of organic salts.

Before long FRANK's ideas were challenged. Many of his contemporaries made significant contributions to the subject, others were futile. STAHL, of Jena, made an important advance when in 1900 he published a paper entitled "Der Sinn der Mycorrhizenbildung" in which the physiological aspects of mycorrhiza were again discussed. He was quite convinced that the mycorrhiza is beneficial for the absorption of mineral nutrients from the soil.

When the endotrophic mycorrhizas of orchids were studied some new and important discoveries of the interrelationships of the partners were made. GALLAUD showed (1905) that the intracellular hyphae of the fungus thrust branches into parenchyma cells of the root, where they developed into profusely branched "arbuscules", and that the root cells ultimately digested these branches.

GALLAUD regarded the endophytes as "internal saprophytes", which, by their haustoria, received nutritive substances from the parenchyma cells into which they penetrated. He could only see a competition between the invading fungus and root cells which, due to their digestive ability, could defend themselves. He saw little to indicate a true biological symbiosis. NOEL BERNARD obtained (1903) significant results from a study of the rôle of endophytes in the germination and growth of orchid seeds, showing that infection was necessary for successful germination. In contrast to the forms which GALLAUD described, BERNARD discovered intracellular mycelia which formed skeins or, in some cases, conidial-like chains of short segments. Prolonged cultivation of the fungus outside of the host so attenuated it that infection, if it took place, was ineffective. Orchid seed germination in nature or in horticultural practice was always associated with fungal infection. BERNARD's observations and conclusions threw much-needed light upon the subject of parasitism and symbiosis, and opened new lines of work.

RAYNER initiated (1915) investigations on the endophytic mycorrhiza of *Calluna* which showed that root infection is an important biological factor in controlling growth. So universal is the association of the fungus, and so necessary for complete development of the plant that she described it as a case of "obligate mycotrophy".

The proliferations of roots caused by invading organisms, which had long been known, received renewed attention after HELLRIEGEL and WILFARTH's demonstration of the rôle of bacteria in producing the legume nodules. Some of the later investigators discovered phenomena of importance, and others completely missed the target. NOEL BERNARD attacked the problem with a view to learning something of the morphogenesis of the general phenomenon of tuberization among plants. His results with orchids were suggestive of a tuberizing effect of a commensal fungus in certain orchids, and, before his untimely death, he attempted to investigate the complicated problem of potato tuber formation. Although tuber formation could be accelerated by the introduction of certain fungi into the soil, he found that they were not indispensable, moreover, commensal fungi are not usually found in tubers of the cultivated potato. MAGROU found that potatoes growing close to *Solanum dulcamara,* which was infected, acquired a mycorrhizal fungus.

The mycorrhiza of trees, both coniferous and broad-leaved, was studied experimentally by MELIN beginning in 1917. The scope of his investigations was broad enough to include many aspects theretofore untouched. He discovered that the mycorrhiza of pine roots differ in mode of branching, color, and internal structure according to the commensal fungus involved, the humus content of the soil, and other edaphic conditions. One of MELIN's early noteworthy accomplishments was the identification of the fungi involved

in the production of the mycorrhiza of various Swedish forest trees, and the experiments in which he proved their symbiotic relationships by syntheses. It is true that NOACK and others had previously assigned a rôle in mycorrhiza formation to various fungi, based upon observations, but MELIN proved the relationship by the synthesis of mycorrhiza by pure culture methods. He also gave especial attention to the short forked roots of the pine ("Gabelmycorrhiza") and discussed problems of virulence and infective powers as far as the data permitted. Later MELIN offered evidence to show that the mycorrhizal association of fungus and root afforded small, but necessary, amounts of growth-promoting substances of the nature of hormones. Birch and aspen mycorrhiza show practically the same structure, according to MELIN (1923), and are of the ectendotrophic type, and are commonly associated with two species of *Boletus*. He could see no obligate relationships, however, with the juvenile stages of the trees. MELIN concluded that the mycorrhiza are beneficial to the tree through their ability to absorb nitrogen compounds from the soil, though he found no evidence that they can fix free nitrogen.

The anatomy and morphology of the coralloid mycorrhiza roots differ in many ways, according to HATCH and DOAK (1933), from that of the slender, long type of roots which extends the root system of the tree.

The beneficial effects of mycorrhizas which were demonstrated in many instances suggested that some of the findings might be applied to silvicultural problems. It has been known that tree growth on certain types of humus is slow and the trees are short-lived. MELIN gave (1925) reasons for attending to the humus-layers in the forests and to the general soil conditions which would favor the development of mycorrhiza. The initial attempts to improve the growth of seedlings in the nursery were not, however, uniformly successful. MCARDLE concluded (1932) that there was no effect, either beneficial or detrimental, of the presence of mycorrhiza on the roots of seedlings.

RAYNER'S work in England has given evidence that inoculation of the seed beds with the proper humus improved the growth of seedlings. She reported (1934) that Scots pine, Corsican pine, and others made better growth in the first year following implantation of small amounts of suitable material containing active mycorrhizas of the species planted, though the superiority of the treated trees later vanished due to soil factors inimical to the development of the symbiotic relationship.

Further work supported MELIN'S observations on the growth of pine seedlings which showed (1927) that the balance between the two partners was determined by soil conditions. REED and FREMONT reported (1935) that the nature of the mycorrhiza of orange roots depended upon the fertilizers applied to the soil.

Fungi parasitic on animals:- Works on systematic mycology often give scant attention to the fungus pathogens of animals, though the existence of mycoses caused by Aspergilli and other fungi has been known for many years. Fungi of this class are characterized by their high temperature optimum. SABOURAUD'S comprehensive work, published in 1910, focused attention on the

scientific aspects of a neglected subject, and stimulated further researches in this field of mycology.

In 1839 LANGENBECK demonstrated fungi in material taken from a patient with thrush and SCHOENLEIN discovered the cause of favus. GRUBY described the cause of *tinea circinata* in 1842 and TILBURY FOX described *tinea pedis* in 1870. VIRCHOW showed (1856) that Aspergilli could develop in the human lungs and in the air-passages of birds, entering, no doubt, with atmospheric dust.

In 1894 RIXFORD described a pulmonary infection in man and in 1896, he showed that the causal agent is *Coccidiomyces immitis*. The acute infection has been reported only from the San Joaquin valley in California. The fungus has been isolated from soil, from vegetation, and from the internal organs of slaughtered cattle and sheep.

The fungus *Actinomyces bovis* has been known, since 1877, as the cause of lumpy-jaw of cattle and of swellings in the bodies of pigs and men. The disease is more prevalent among men engaged in agricultural pursuits and in the majority of cases is localized on the head and neck. The genus *Actinomyces* has an uncertain position among the fungi, since they sometimes resemble bacteria and at others mold fungi. *Acharion Schoenleinii* is the cause of favus, a disease of the skin, chiefly of the scalp, characterized by yellowish, dry incrustations of more or less circular form, composed of the sporules and mycelia of the fungus. Favus occurs chiefly in Russia and other European and Asiatic countries.

The dermatophytosis of the human foot ("Athlete's Foot") which occurs over much of the United States is caused by a fungus variously designated *Trichophyton gypseum, T. interdigitale,* or *T. pedis.* Several species of *Trichophyton* infect the human skin causing various lesions popularly called Ringworm. In the case of *tinea tonsurans,* the hair folicles are affected and the hairs are seen to be twisted and bent. Sometimes the hair shaft contains a mass of fungus spores. *Monilia albicans,* the cause of thrush, was described by ROBIN in 1843 under the name *Oidium albicans.* The organism is probably a weak pathogen, but once a diseased state is established, the condition is apt to persist indefinitely. The organism is more likely to find suitable conditions for infection in persons whose skin is softened by frequent or prolonged immersion in water.

The encyclopedic works on mycology:- The necessity of assembling and classifying the information about fungi has impressed itself on many students of the subject, but few have undertaken the arduous task of compiling it. The encyclopedic works prepared in recent years have had to face the task of organizing a vast collection of works dealing with many aspects of mycology.

A few of the useful compilations may be mentioned.

P. A. SACCARDO collected and published descriptions of species in "Sylloge fungorum omnium hucusque cognitorum" in 18 volumes (1892-1906), eventually adding supplementary volumes. This is perhaps the last great mycological work to be written in Latin. W. G. FARLOW assembled the parasitic fungi of the United States according to their hosts in "A provisional host index" (1888-1891); and SEYMOUR has published an enlarged edition of the same (1929)

since FARLOW's death. A large compendium of the parasitic fungi of Europe arranged according to their hosts, the "Enumeratio systematica fungorum" (1919-1924) in 5 volumes started by C. A. J. A. OUDEMANS was completed by J. W. MOLL and others. The volumes on fungi in ENGLER and PRANTL's "Natürlichen Pflanzenfamilien" and in the second edition of RABENHORST's "Kryptogamen Flora Deutschlands", both prepared by specialists in their fields, have collated important material on mycology. DE BARY, in the second edition of "Vergleichende Morphologie . . ." (1884), assembled and critically discussed the important works on the biology of fungi, bacteria, and mycetozoa which had hitherto been published. The important handbook of W. ZOPF entitled "Die Pilze" (1890) contained, not only original contributions, but a discussion of the work of many other investigators.

LAFAR published (1904-1914) his "Handbuch der Technischen Mykologie" which is devoted essentially to a discussion of the physiology of microörganisms. The "Handbuch" was an important aid to workers in the fermentation industries like dairying, enology, brewing, and pharmacy.

A retrospective glance at the development of mycological work suffices to show that the group of organisms which began to be investigated scientifically at the beginning of the 19th century has been found to be a large and important group of plants. In ways little suspected at the beginning they are known to have a significant place in the cycle of organic life. Their activities are intimately concerned with processes of growth and decay, health and disease, life and death.

The following chapter will present a brief summary of the development of the knowledge of plant pathology and will discuss additional mycological development.

REFERENCES:-

ARTHUR, J. C. (1929): The plant rusts. Wiley, New York.

BERKELEY, M. J. (1860): Outlines of British fungology. Reeve, London.

DE BARY, ANTON (1884): Vergleichende Morphologie und Biologie der Pilze, Mycetozoen und Bakterien. Engelmann, Leipzig. (Transl. by GARNSEY, 1887, Clarendon Press, Oxford).

FRIES, E. (1821-29): Systema mycologicum. Ex offic. Berlingiana, Lund.

GÄUMANN, ERNST (1926): Vergleichende Morphologie der Pilze. Fischer, Jena. (Transl. by DODGE, 1928, McGraw-Hill, New York).

GUILLIERMOND, A. (1920): The yeasts (transl. by TANNER). Wiley, New York.

HARDEN, A. (1911): Alcoholic fermentation (Valuable bibliography). Longmans, Green, London.

LAFAR, F. (1904-1914): Handbuch der technischen Mykologie . . ., Vols. 1-5, Fischer, Jena. (Transl. by SALTER, 1903-1910).

LARGE, E. C. (1940): The Advance of the Fungi. Holt, New York.

LINDAU, G. et SYDOW, P. (1908-1917): Thesaurus literaturae mycologicae et lichenologicae. Borntraeger, Berlin.

LÜTJEHARMS, W. J. (1936): Zur Geschichte der Mykologie des 18. Jahrhundert (Diss. Leiden).

PERSOON, C. H. (1801): Synopsis methodica fungorum. Dieterich, Göttingen.

RAYNER, M. C. (1927): Mycorrhiza. Wheldon and Wesley, London. (With valuable bibliography).

SACCARDO, P. A. (1882-1931): Sylloge fungorum omnium hucusque cognitorum, Vols. 1-25. Patavii (Continuation by A. TROTTER).

TULASNE, L. R. and C. (1861-65): Selecta fungorum carpologia (Transl. by GROVE and SHEAR, Oxford U. P.). Parisiis in Imp. Typogr.

Chapter XIX.

PLANT PATHOLOGY.

The idea of disease in plants had a beginning in the days when the nature of the vegetable world was imperfectly understood, and the role of micro-organisms unsuspected. Many years were destined to pass before plant pathology became a subject which was scientifically investigated. The first important discoveries were made by several amateurs who could see that some extraneous agent produced deleterious effects on an otherwise normal plant. Although much of the work of those pioneers was empirical, it had the merit of being experimental. Their successors eventually described organisms and demonstrated causal relations to pathological conditions, showing that it is important to study the life-history of the micro-organism in relation to its pathogenesis. Historically, it is of great interest to note that the role of micro-organisms in disease in plants was discovered some years before their relation to animal diseases was recognized.

An epoch of discoveries (1750-1850):- The illustrious work of MATTHIEU DU TILLET on the bunt of wheat is an example of the way in which this epoch started. The Academy of Bordeaux in 1750 offered a prize for the best dissertation on the bunt of wheat. One year later TILLET, who was director of the mint of Troye, began his experiments on the problem in which he included tests on the nature of the soil, the manures applied, time of seeding, quality of the seed, and the effects of various seed treatments. He soon found that the cause of the "corruption" was on the wheat seed and, in some cases, in manure containing straw from infected wheat fields. He thought that the black dust of bunted wheat might contain a "virus" which could infect healthy wheat; an idea which he confirmed by infecting clean seed with black dust from bunted wheat, thereby obtaining more bunted heads than in any other experimental plot.

TILLET used an admirable technique of plot experimentation, including an abundance of untreated plots, replicate treatments, and an adequate system of records. He published the results of his work in 1755 in his "Dissertation sur la cause qui corrompt et noircit les grains de bled dans les épis et sur les moyens de prévenir ces accidens", and received the prize offered by the Academy of Bordeaux. In a supplement to the dissertation he recommended the following treatment for the prevention of the bunt: wash the grain in flowing water, dry the grain in the sun, wash it in lye, dry it again, sprinkle it with lye, and dust with lime. He had the honor of presenting his results to LOUIS XV who, wishing to see the actual experiments, commissioned him to conduct experiments at Trianon. Impressed by the success of TILLET's experiments, the king published pamphlets containing the recipes for the

control of wheat bunt and ordered them to be distributed throughout the kingdom.

The extraordinary investigations of BENEDICT PRÉVOST (1755-1819), a native of Geneva, on the bunt of wheat opened the way for fundamental progress in plant pathology. As far as he went he was correct in his interpretation of the role of organisms as pathogenic agents. He was not only scientifically sound in his microscopical work, but also carried out the technical work which led to the discovery of methods for seed disinfection. He published "Mémoire sur la cause immédiate de la carie ou charbon des blés . . ." (1807) in which he correctly described the spores of *Tilletia tritici* and their process of germination in both water and air. He succeeded in infecting wheat seed with the bunt fungus and recovered its spores from the kernels of the affected plants. After experimenting with many substances for disinfecting seeds prior to sowing, he demonstrated the efficacy of copper sulfate, finding that a concentration of 1 to 10,000 killed the fungus spores without notable injury to the wheat seed. He then conducted field experiments to compare the effects of different treatments.

PRÉVOST finally made the sapient observation that if copper sulfate treatment of seed wheat were adopted only by a small number of careful farmers they would harvest bunt-free wheat which might, without further treatment, be planted. In this way he foresaw that they could eventually eliminate the germ of infection from the soil.

The age-old plague of wheat rust which for long years had robbed the husbandman of his harvests and his children of their bread had never ceased to command attention. It was perhaps logical that the farmers should have comprehended the relations between rust and barberry bushes better than the botanists of their time. When at length men began to make a few simple infection experiments, they were impelled to some extent by the bitter controversies then raging between those who wished to eradicate the barberry and those who maintained that the diseases on barberry and wheat were totally unrelated. THOMAS ANDREW KNIGHT (1759-1838) made one of the first reliable experiments on this problem in 1804 when he infected wheat with the rust by transferring spores from barberry as well as from rusted wheat leaves. There is little evidence, however, that his discovery led to any important results. KNIGHT contributed a paper in 1834 on leaf curl and red spider injury of the peach, in which he reported that both diseases were controlled when the trees were sprinkled in early spring with "water holding in solution or suspension a mixture of lime and flowers of sulphur". JOHN ROBERTSON's observations on the powdery mildew of the peach and his recommendations anticipated, in a way, the work of modern plant pathologists. In 1821 he concluded from his infection experiments that the disease was due to the action of a fungus and demonstrated that it could be cured by applying sulphur suspended in a soap solution.

F. UNGER (1800-1870) reverted to the autogenetic conception of plant diseases, and, like the scholastics, he made no experiments. "Exanthema" was the name he applied to the eruptions observed on diseased plants. He published (1833) an exposition of his ideas on plant diseases in a work entitled "Die Exantheme

der Pflanzen . . ." and he illustrated subsequent memoirs with really meritorious drawings. He retained, however, the old idea that the fungi were engendered by the disease and appears to have believed that the filamentous hyphae were the congealed sap of the plant. He maintained that the *vera causa* of disease was an unbalanced nutritive condition due to abnormal weather or water relations. It is hardly credible that he should have made such bizarre statements after having clearly seen the morphology of other anatomical features in plants. WIEGMANN and MEYEN were contemporaries of UNGER, but since they saw effects rather than causes neither added anything worthy of comment to the subject. The stultifying influence of the dogma of spontaneous generation manifests itself in all the work of the "autogeneticists".

The science of plant pathology was not started until the epoch-making work of DE BARY had given an account of the life histories of important fungi and defined terms like "parasitism", "resistance", "infection", etc. As already mentioned in the preceding chapter, DE BARY gave a rational basis for plant pathology. His work on "Die Brandpilze" and the potato disease established the fact that definite diseases are caused by definite organisms, and he rightly interpreted what had baffled many others. Similarly the brothers TULASNE who published their investigations on the smuts in 1847, and their investigations on the development of ergot in 1853, have also been discussed.

The work of JULIUS KÜHN (1825-1910) on plant pathology supplemented in many ways the mycological discoveries of DE BARY. KÜHN had studied first at Poppelsdorf-Bonn, then at Leipzig, receiving from the latter University his doctor's degree in 1856. After spending a few years as manager of a large estate in lower Silesia he accepted a call to Halle in 1862. The publication in 1858 of KÜHN's book entitled "Die Krankheiten der Kulturgewächse . . ." marked a new era in plant pathology. Having obtained a scientific training, he comprehended the etiological factors in plant disease. Deeply interested in the life histories of causal organisms, KÜHN also recognized the adverse physical agencies due to climatic and soil factors. While holding the chair of agriculture at Halle he wrote important papers on a variety of other agricultural subjects. His eminence, as an agricultural scientist, depends however chiefly on his successful work as a mycological plant pathologist, in which field he initiated many profitable lines of work.

An epoch of expansion:- Investigations in plant pathology in the half century following its founding by DE BARY and KÜHN were devoted principally to studies of the life histories or, as often termed, biological relationships of fungi. The emphasis on mycological work was necessary and was justified by the knowledge thereby gained of the modes of reproduction, dissemination, and infection from studies in controlled cultures and in the field. It is conservative to say that plant pathology had a great vitalizing influence on mycology in the 19th century. The names of other mycologists who did pioneer work in plant pathology must be noted.

EDOUARD PRILLIEUX (1829-1915), professor of botany at the Institut National Agronomique of France was the organizing force

in plant pathology in his time and the first director of the French laboratory for plant pathology. ALEXIS MILLARDET (1838-1902), who published his first paper on plant pathology in 1865, was commissioned by the French government to investigate two serious diseases of the vine which had been introduced from America, *viz.*, phylloxera and the downy mildew caused by *Plasmopara viticola.* He was at that time professor of botany at the University of Bordeaux. His well-known discovery in 1883 of the efficacy of a lime-copper sulfate mixture (of which more will be said later) as a fungicide grew out of his work on the mildew. His introduction of resistant American stocks on which the European varieties were grafted solved the phylloxera problem. Many other works on the etiology of plant diseases came from his hand. WORONIN's brilliant work in Russia has been previously mentioned.

JAKOB ERIKSSON (1848-1931). for many years professor and director of the botanical division of the Central agricultural experiment station in Stockholm promoted the study of plant pathology, especially the diseases of cereals, in Sweden. In 1894 he made the first announcement of physiological races in the rust fungi. He was also the proponent and main supporter of the "mycoplasm theory", according to which the protoplasm of the pathogen lives for a time in a simply organized form as a plasmodium in the cells of the host. If conditions are appropriate, this "mycoplasm" migrates from the cells into the intercellular spaces, secretes a wall on the surface of the body, and develops into a mycelium. Although this novel theory has received considerable attention from pathologists, it still lacks confirmation.

In Italy plant pathology has been advanced by many workers, among whom may be mentioned BERLESE (1864-1903), COMES (1848-1917), SAVASTANO (*b.* 1853), and PETRI (*b.* 1875). In addition to KÜHN and DE BARY the development of plant pathology in Germany owes much to FRANK (1839-1900) who carried the results of scientific work into agricultural practices.

Plant pathology owes its establishment in Japan to K. MIYABE (*b.* 1860) who, in 1894, began to give courses in the subject in the Sapporo Agricultural College.

In North America etiological work on plant diseases spread from FARLOW's laboratory at Harvard University and from the United States Department of Agriculture at Washington. Work in the latter laboratory was initiated when F. L. SCRIBNER in 1886 was appointed chief of the section of mycology. The activities of the laboratory were then concerned with the utility of copper sulfate sprays for the control of grape diseases.

Among the early problems of this department of agriculture were some of uncommon perplexity. The baffling disease known as the California Vine Disease, which was studied by NEWTON B. PIERCE and described in 1892, is one of a class of maladies which stimulated a vast amount of work in America and in Europe. No one succeeded in finding the causal agent. PIERCE studied the general and local effects of the disease. VIALA and SAVAGEAU described (1892) the anatomical features of the California Vine Disease with great care and concluded that a myxomycete to which they gave the name *Plasmodiophora californica* was the causal agent. Their conclusions were not however confirmed. Great credit should be awarded to PIERCE for his pioneer work in a field

laboratory remote from the central offices of the department of agriculture in Washington.

At the beginning of the 20th century many other centers developed in the United States in governmental stations and in universities. The work of investigation and instruction at the universities of Minnesota, Wisconsin, and Cornell, and the researches of the Bureau of Plant Industry had an important influence on the development of plant pathology. The American Phytopathological Society was organized in 1909 and its journal "Phytopathology" began to be published in 1911.

Forest pathology has had its greatest development in European countries where for many centuries the culture of timber trees has received attention. The first important publications on the diseases of forest trees were by WILLKOMM, HALLIER, SORAUER, and FRANK. WILLKOMM, in his book, "Die Mikroskopischen Feinde des Waldes" (1866-1867), gave an account of his observations upon the red rot and white rot of timber. He observed different kinds of hyphae in rotting wood, but failed to connect them with the fruiting bodies of the fleshy fungi. Obviously, he added little that was new to the subject. His work shows how incompletely the decay of wood was then understood.

It remained for ROBERT HARTIG (1839-1901) to develop the subject of the diseases of forest trees in a scientific manner. HARTIG was a professional forester and naturally well acquainted with field conditions which influence the susceptibility of trees to the invasion of pathogens. In his two classical publications, issued in 1874 and 1878, he described not only the causal organisms but also their actions on the cellular constituents of the wood, indicating how they caused disintegration and decay. He showed that each fungus has a specific action upon wood, so that it is often possible by macroscopic inspection of a piece of wood to determine the fungus concerned in the decay, even in the absence of the fruiting body. He included the biologic and ecologic factors in the etiology of the disease. In his "Lehrbuch der Pflanzenkrankheiten", HARTIG devoted page after page to the injuries caused by invading pathogens and the specific types of response on the part of the tree to the continued presence of the invader; whether they were due to decay or to hypertrophy of growth, all were carefully described and pictured. These phenomena were more readily studied in trees than in annual plants. He gave especial attention to the healing of wounds and the production of new tissues in general, pointing to the protective action of resinous exudates, as well as of tannin, in trees. His work on the dry rot of timber caused by *Merulius lacrymans* (1885) explained the cause of extensive losses to lumber and of the decay of joists in buildings. HARTIG's inspiring example led to active research by other students of the fungi.

The English botanist, BULLER, investigated the decay of the sycamore, isolating and identifying enzymes which caused decay and disintegration of the wood. Clarifying work in forest pathology was also carried on by VON TUBEUF, one of HARTIG's students. His textbook, of which an English translation entitled "Diseases of Plants" appeared in 1897, is noteworthy for the descriptions and illustrations of many diseases of forest trees. The idea of describing scientifically the abnormalities due to the presence of a para-

sitic invader belongs properly to HARTIG. Prior to his time, almost no one had paid any attention to the real pathogenesis or pathological symptoms. Since his time, however, there has been a growing tendency to describe carefully the cytological and morphological changes induced by plant parasites. E. ROSTRUP (1831-1907) of Denmark also belongs to this period in which the etiology of forest tree diseases was thoroughly studied from the standpoint of mycology.

The appearance of papers about 1900 by ATKINSON, VON SCHRENK, and SPAULDING may be said to mark the beginning of scientific forest pathology in the United States. The Federal Department of Agriculture established a laboratory of forest pathology in 1907, in which problems concerned with epidemics of parasitic fungus diseases of timber trees have been investigated, as well as problems of timber decay.

A brief account of the work of this laboratory on two destructive tree diseases seems warranted in this chapter, because of their historical importance.

The "Chestnut blight" caused by *Endothia parasitica,* first noted in 1904 on trees in the New York Zoological Park, spread with great rapidity on the native chestnut, *Castanea dentata,* and, before its serious nature was appreciated, had infected thousands of trees in New York and adjacent states. In little more than ten years, it had become established in the chestnut forests of the Appalachian region. The public was aroused as never before to the importance of forest diseases. Unfortunately the disease had become widely distributed before intensive control work could be started, and detection of infections on trees was exceedingly difficult. Federal and state officials, nevertheless, put up a valiant fight against the epidemic, in which pathologists and foresters utilized the best available means for combatting this virulent disease. Eventually they were obliged to relinquish their attempts.

The second tree disease which has notable historical importance in the history of plant pathology is the "White pine blister rust", a disease which attacks the five-needle pines. The appearance of the disease in North America was a matter of grave concern to foresters and timbermen. The disease, which probably came from Asia, was first found in Europe in 1854, reached the United States about 1898, and was found in New York in 1906 on European black currant and in New England in 1915 on native pines. It appeared in British Columbia about 1910 and was discovered at Vancouver and in western Washington in 1921. In 1938 the disease was established in every state on the northern border of the United States with the exception of North Dakota. In the east it extended as far southward as Virginia and in the west into California. The "White pine blister rust" is caused by the heteroecius fungus, *Cronartium ribicola,* which lives alternately on the five-needle pine and on *Ribes* species (currants and gooseberries).

Detailed information about the epidemiology of the disease is a prerequisite for any attempted control measures. The control of "White pine blister rust" is highly successful because based on the fact that spore distribution is wind-borne. Although the aeciospores are carried very long distances from the pine, the teliospores are carried very short distances from the *Ribes.* Knowledge of facts such as these makes it possible to decide when and where

control measures should be attempted, or are likely to end in failure.

These two examples are mentioned to show some of the ways in which national governments undertake to control the progress of serious epidemics which threaten important plant products. Nothing like this was known or attempted a century ago. While success has been far from perfect, it is thought that by the study of these introduced epidemics and by experimental control, better methods can be worked out.

Bacterial diseases:- When it was discovered that a small but important group of plant diseases is caused by bacteria the scope of plant pathology was considerably widened. DE BARY made brief mention of this class of diseases in his "Vergleichende Morphologie und Biologie . . ." (1884), but said that more extended study of the phenomenon was advisable. Plant pathologists of that time were cautious about recognizing the role of bacteria as plant pathogens since they knew that all sorts of bacteria could be present on the surface of plants and that saprophytes often invade necrotic tissues. Moreover, bacterial pathogens (as is now known) are often characterized by slow growth, hence their isolation is difficult.

The first bacterial plant disease was discovered in 1878 by T. J. BURRILL, professor of botany at the University of Illinois. He discovered that the Twig Blight of pear, apple, and other pomaceous trees is caused by a parasitic bacillus which kills the cells of the cambium layer. BURRILL named the organism *Bacillus amylovorus*. This discovery was made only two years after KOCH had demonstrated the causal relation between a definite bacillus and anthrax, and ten years before BEIJERINCK discovered the organism of the legume nodule. Later experiments made by ARTHUR and by WAITE, using more refined methods, confirmed the essential features of BURRILL's pioneer work. J. H. WAKKER, working at Amsterdam, discovered (1883-1884) that the "yellow disease" of hyacinths is caused by an organism which he named *Bacillus hyacinthi*. The disease is caused by an organism which multiplies chiefly in the fibrovascular system and progresses very slowly; often the host plant is not killed for a year or more. WAKKER's papers were among the first of scientific importance in the literature of bacterial plant diseases.

After a suitable technique had been developed and some aggressive workers entered the field, the science of phytobacteriology made rapid progress. E. F. SMITH, an American pathologist in the Federal Department of Agriculture, discovered (1893-95) that an organism to which he gave the name *Bacillus tracheiphilus* is the cause of a destructive wilt disease of cucurbits. The bacillus grows only in the fibrovascular bundles of the *Cucurbitaceae* and produces in them a white viscid mass which interrupts translocation. The infection is carried by phytophagous insects like *Diabrotica vittata*. NEWTON B. PIERCE demonstrated (1893) that an unknown bacterium was constantly associated with the blight of cultivated walnuts (*Juglans regia*) in California. He first isolated the organism and published a description of the disease — *Pseudomonas juglandis*. PIERCE made a study of the resistance of various hosts to the organism. The organism was proved to be pathogenic to nuts, leaves, and tender branches of the walnut tree. L. SAVAS-

TANO, in Italy, discovered (1886-1887) a cultivable organism (*Ps. oleae*) in the interior of young, growing olive galls. Later he succeeded in infecting healthy trees with pure cultures of *Ps. oleae* and in demonstrating the etiological relation of the microörganisms to the disease.

E. F. SMITH and C. O. TOWNSEND demonstrated (1907) that a previously unknown *Pseudomonas* is the cause of Crown Gall of trees. This microörganism produces characteristic hypertrophies in young tissues resembling those of the olive galls studied by SAVASTANO. In subsequent years SMITH and his associates prosecuted further studies on the pathology of the disease and suggested important analogies with cancer of the human body. SMITH attempted to correlate cell proliferation in crown gall with the production by the causal organism of an irritating product such as acetic acid; it was recently shown that indolacetic acid is produced by *Ps. tumefaciens* and that it stimulates cell proliferation. Although the crown gall organism for many years had defied all attempts towards its detection in the crown gall tissues, more is known about it now than about any other bacterial plant pathogen.

ARTHUR and GOLDEN described (1892) a bacterial disease of sugar beets in Indiana, and soon thereafter the Black Rot of cabbage was investigated independently in America by PAMMEL, RUSSELL, and E. F. SMITH, and by VAN HALL in Holland. O. APPEL of Berlin made the important discovery (1903) that *Bacillus phytophthorus* is the organism which causes the serious disease of potatoes called "Black Leg". This disease attacks both stems and tubers of the host plant and is quite prevalent in America and Europe. Tubers which appear sound externally are often infected internally and if used as seed tubers the following year transmit the infection.

Citrus canker is a bacterial disease of uncommon virulence on some species of citrus trees in certain countries. It was apparently introduced from the Orient into the United States about 1911, but was not recognized as a new disease until 1913. The causal organism, *Phytomonas citri* Hasse, which causes lesions on leaves, twigs, and fruit, was unknown to American pathologists and the disease was confused with citrus scab.

Since no one at the time realized the uncommon infectiousness of the disease, it spread rapidly in the southeastern United States, but the gravity of the situation was soon apparent. Neither the states concerned nor the citrus industry were prepared to cope with the emergency. The Federal Government, therefore, acting in concert with the other agencies, provided funds for interstate activities. As a further protection the Secretary of Agriculture declared a quarantine, effective Jan. 1, 1915, prohibiting the importation of citrus nursery stock, buds, scions, or seeds into the United States from foreign countries. Efforts to check the spread of the disease by complete defoliation of the infected stock followed by immediate treatment with a fungicide were ineffectual. The organism is so virulent that contact of men or animals with diseased trees spread the disease and thus defeated the object of the work. Success was only achieved by destroying the trees by spraying them with burning oil.

The campaign against citrus canker was comparable to the attacks made in recent years on certain diseases of the human

race. The control measures required were more drastic than had been theretofore applied to epidemics of plant diseases. The cost in state, federal, and private funds was more than $2,500,000 and upwards of 4,000,000 trees were destroyed. The successful eradication of citrus canker in the southeastern United States in a brief period was such a unique episode in modern plant pathology that mention is justifiable in this place, since it saved a fruit industry of major importance.

Resistance and immunity:- One of the important concepts evolved from the study of parasitism is the resistance of the majority of plants to infection. The earlier mycologists and pathologists appear to have been blind to the importance of the phenomenon until DE BARY produced his illuminating works. He analyzed it with respect to (a) the attack of the parasite on its host, (b) the course of further growth taken by the parasite after entry, (c) the reactions of the host after its occupation and the results of the reciprocal action of the two symbionts.

DE BARY elucidated the factors that are responsible for susceptibility or resistance in connection with the life of facultative parasites. He demonstrated that some fungus spores germinate only when in contact with their host plants, and called attention to the fact that the mycelia of some obligate parasites are confined to the immediate point of attack, while others spread widely from the point of infection over or through the host. DE BARY and others concerned with the etiology of diseases caused by parasites clearly stated that infection often occurs only when the host plant is very young. Congenital ability of the host to withstand infection is termed resistance. The modern knowledge of susceptibility and resistance has been summarized and greatly clarified by MORSTATT in the 6th edition of SORAUER's "Handbuch der Pflanzenkrankheiten".

Resistance has been investigated with reference to the morphology, genetics, cytology, and physiology of the host plant. The most obvious type of host resistance is associated with some morphological or anatomical character, and was earlier assumed to be the only important type.

It was assumed that plants possessing a heavily cutinized, or waxy epidermis, or a corky stem, were resistant to invasion by parasites. The idea was supported by SAPPIN-TROUFFY who discovered (1896) that the mycelium of *Puccinia graminis* is restricted to the chlorophyllous parenchyma, and does not develop in the collenchyma. The growth of the mycelium of the fungus was correspondingly restricted when the parenchyma was small in comparison with the amount of collenchyma. ARTHUR affirmed the idea by his observation (1902) that the mycelia of certain rusts may be limited in their development by the anatomical nature of the tissues of *Spartina*. On the contrary WARD concluded (1902) that morphological characters of *Bromus* had little effect on rust resistance and COBB reported (1892) that the relative hairiness of resistant wheat varieties was not sufficient to explain their resistance to rust. BREFELD (1839-1925) and others discovered that infection of wheat flowers by bunt spores occurs through the stigma of the flowers. The spores which reach the stigmas germinate there, producing germ tubes which grow into the ovules. Investi-

gations have shown that immunity to bunt infection in some varieties of wheat is due to the way in which the glumes completely enclose the flowers and prevent the bunt spores from reaching the stigmas during the susceptible time.

The consensus of ideas has been that other types of resistance are of more importance than the morphological characters of the host. Genuine resistance to disease is undoubtedly linked to hereditary factors. The genetical relations of resistance which have been investigated indicate that it is inherited as a dominant Mendelian character, as a few chosen examples will show.

When *Kanred* (a resistant variety) and other varieties of common wheat were crossed by MELCHERS and PARKER they found (1922) that the resistance to certain physiologic races of *Puccinia graminis* was inherited in the ratio of three resistant to one susceptible descendant. MAINS and LEIGHTY found (1923) rye plants which manifested high resistance to leaf rust, *P. dispersa.* HENRY reported (1926) that the resistance of flax to *Melampsora lini,* inherited as a dominant character, showed in some crosses a ratio of 3:1, but in others a ratio of 15:1. MAINS (1926) and others have shown that resistance to various rusts may be separately inherited and also that the host-resistance of varieties to different physiologic races of rust fungi may be inherited separately. EMSWELLER and JONES who studied the resistance of the cultivated snapdragon, *Antirrhinum,* to *Puccinia antirrhini* found (1934) that all plants in the F_1 generation were resistant to the rust. When an F_1 hybrid plant, free from modifying genes, was self pollinated, the ratio of resistant to susceptible plants of F_2 generation was 3:1. FAHMY demonstrated (1936) that all the F_1 descendants of crosses of immune and susceptible cotton plants were immune to the *Fusarium* causing wilt in Egypt. In the F_2 generation segregation occurred giving an average of 75 per cent phenotypic immunes, 15 per cent of tolerants, and 10 per cent of susceptibles. WALKER has concluded (1935) that the resistance of flax, tomatoes, tobacco, and other plants is due to a complex genetic basis, while in the pea and others, resistance is controlled by a single gene. He found two types of resistance in cabbage—one which is controlled by a single gene, the other genetically complex. Additional study will probably show how environmental conditions affect these types of resistance in fungus diseases. The recent discoveries of clons resistant to other diseases will be discussed in connection with work on the selection and breeding of resistant varieties.

Physiological factors in resistance and susceptibility are not always easy to determine though they have been recognized for a long time. The conditions due to the weather and season have very intimate effects not only on the susceptibility of plants to infection but also on the propagation of parasitic organisms. The devastating epidemic of the late blight of potatoes in 1845 which caused famine and suffering in Ireland is said to have been associated with weather conditions in the summer and autumn of that year. Detailed information concerning the relation of the internal physiological factors which affect the resistance of the host to infectious agents is remarkably meager. Only a few cases can be cited and they show that investigations of the phenomena have scarcely begun. BUTLER considered that immunity is the end

point in an ascending scale of resistance, but others define the term differently. A distinct type of immunity was discovered (1915) by REED and CRABILL in apples escaping infection from *Gymnosporangium*. The immunity is actually due to hypersusceptibility, as shown by the rapid death of host cells surrounding the centers of infection. The mycelium of obligate parasites fails to develop in such cases because it meets a barrier of dead host cells.

ANGELL, LINK, and WALKER found (1930) that resistance of onions to *Colletotrichum circinnans* is associated with their content of water soluble protocatechuic acid and catechol, both of which are strongly toxic to the fungus mentioned. Evidence given in 1930 by DUFRÉNOY and others indicated that the natural immunity of many plants may be due to phenolic compounds which appear to be formed rapidly in cells penetrated or surrounded by invading parasites. The cells of a barrier either by their phenolic contents, or by their reactions, exercise a detrimental effect on the pathogens. It is well known that injured sap wood of coniferous trees secretes large amounts of resinous substances which are often effective in preventing the spread of parasitic invaders. FISCHER and GÄUMANN have restricted (1929) the term immunity to cases in which the host plant acquires the ability to withstand infection as the result, either of the stimulation by the parasite, or by the production of protective substances. GÄUMANN demonstrated (1933) a local reaction in potato tubers inoculated with *Bacillus phytophthorus*. The excess of temperature, which was but 0.005°C. above the surrounding air in a normal tuber, became 30 times as great as a result of the inoculation, and the amount of CO_2 evolved was correspondingly large. Following the subsidence of temperature and CO_2 production, GAUMANN reinoculated the tubers in another place; in contrast to the former result, there was no definite reaction. He concluded that the ability of the tubers to react had been exhausted by the first attack. The influence of carbohydrate supply on seedling infection of cereals by *Gibberella* is fairly direct. Larger amounts of carbohydrate favor seedling blight without much relation to temperatures. DICKSON showed (1923) that the available carbohydrate content of wheat seedlings was greater at lower temperature but it was greater in maize at higher temperatures.

Satisfactory evidence of acquired immunity from fungus parasites of perennial plants is scanty. BUTLER remarked that the scab diseases of apples and pears caused by *Venturia,* appear annually on the same plants with equal vigor if the weather conditions are equally favorable. Evidence that *Pelargonium zonale* may acquire immunity to *Phytomonas barkeri* was presented (1934) by PASSALACQUA showing that the antigens had apparently caused the formation of the appropriate antibodies.

The alluring hope that resistance might be conferred by the application of chemicals to the soil has not been realized to any great extent. DE PHILIPPIS reported (1932) that beans were immunized by an application of a zinc salt; HOAGLAND and SNYDER reported (1933) a resistance of strawberries to mildew following the addition of certain micro-elements to the culture medium.

Investigations on the resistance and immunity of plants are still incomplete, so it is impossible to make any comprehensive

statements about them. Resistance is known to be hereditary or induced, and may be complete or partial. It may be influenced by histological or physiological conditions, especially by the age of the plant, water relations, and temperature.

Virus diseases:- The discovery of virus diseases of plants and their investigation have in the last 20 years opened a new chapter in plant pathology. The unique nature of the phenomena, the uncertain nature of the infective agent, and the futility of the conventional technique of microbiology hindered for a time the finding of the headlands on the new coast. Eventually the lay of the land became known, but the work of discovery is not completed. It is increasingly apparent that many of the diseases formerly designated "non-parasitic" are virus diseases, and that the continually declining yields of some clons were due to the increasing infection by a virus. The boundaries of the subject are not precisely known, but it appears that studies on the viruses may contribute important information on problems of profound biochemical significance, since viruses appear to share the properties of living and non-living matter.

Omitting a few incidental reports such as the "Breaking" of tulips described by L'ECLUSE in 1576, the first historically significant work on a virus disease of plants emanated from MAYER in 1886. He described then the tobacco mosaic and gave it the name which is still used for describing the mottled type of virus disease. In addition he demonstrated its infectivity by inoculating healthy tobacco plants. E. F. SMITH worked on the enigmatical disease of peach trees called "yellows" and demonstrated (1888) that it could be transmitted by means of budding or grafting. Nothing further was then discovered about the nature of the infective principle.

It remained for D. IWANOWSKI to make an important advance when he demonstrated (1892) that the sap of affected tobacco plants after passage through a bacterial-proof filter tube could infect healthy plants with the mosaic disease. Although he could not demonstrate the presence of an organism in the filtered juice of a diseased plant, he nevertheless considered that the disease was bacterial in nature. Subsequent workers verified IWANOWSKI's filtration experiments and, adopting his criterion, for some time the infective agent was designated as a filtrable virus.

BEIJERINCK, who formulated (1899) the concept of the "contagium vivum fluidum", made the next important advance. By diffusion experiments in agar he showed that the causative agent was water-soluble and that it retained its infectiousness after drying or after precipitation by alcohol. He concluded that it could not be an ordinary bacterium and therefore formulated the hypothesis of a living contagious fluid. He presented evidence that the contagium was carried in the phloem, and that it increased in quantity only in cells which were multiplying. He predicted that other diseases of this kind might be found in plants.

The 30 years which followed BEIJERINCK's work were a period of discovery and description of virus diseases. The symptoms of virus diseases of plants have been described (but without complete agreement) by many authors. The causal agents do not produce anything definite, like spores, which may be used for identification and the effects on the plant may be variously interpreted. In the

absence of more definite information about the virus itself, the diseases were usually distinguished by the symptoms of diseased plants. MAYER applied the term "mosaic" to the affected tobacco plants he investigated and the name has been retained, though now inadequate. E. F. SMITH adopted the name "yellows" by which farmers had long designated the peach disease which was later determined to be a virus disease. TOWNSEND employed the name "curly top" which had likewise been current to designate the disease of sugar beets which is now known to be caused by a virus. Many other instances might be cited.

These names described conspicuous symptoms of the host plant, but, as cases were multiplied, it was apparent that such terms as "crinkle", "curl", or "bunchy top" lacked precision.

HEALD classified (1933) the effects as:

(a) pale color, due to lack of chlorophyll
(b) general reduction in size (dwarfness)
(c) excessive branching (sometimes accompanying b)
(d) premature yellowing and dropping of leaves

K. M. SMITH and BROOKS classified (1934) virus diseases as:

(a) mosaic diseases characterized by chlorosis or mottling
(b) necrotic diseases marked by dead spots, streaks or stripes on leaves or stems
(c) distortion or hypertrophy of all or part of the plant

Other writers have endeavored at various times to make a systematic classification of viruses, but their work has not resulted in complete emancipation of the nomenclature from the chaotic condition into which it was thrown by the rapid discoveries of recent decades. BAWDEN has stated (1939) in a recent work the rationale on which a classification should be based. His work should be consulted for details.

The effects of virus were thought to be most plainly manifested by the vegetative organs of the plant, but additional investigations have broadened the views of their symptomology.

In 1923 PETRI showed that living cells in the root show derangements when the vine is affected with a disease which he later found to be caused by a virus borne in the soil.

The effects of virus are most frequently manifested by the shoot of the plant, the roots frequently being symptomless. HUTCHINS demonstrated, however, in 1927 that the virus of the "phony" disease of the peach occurs in the root although the symptoms are manifested by the tops. It has since been pointed out that other viruses may occur in root and shoot and may be demonstrated by appropriate methods of transmission (juice inoculation, grafting, etc.).

Subsequent investigators have confirmed BEIJERINCK's conclusion that the virus is chiefly located in the living cells of the host plant. It may spread from cell to cell by diffusion, but the movement is slow in the case of certain viruses. It probably travels in the phloem, although the evidence is necessarily indirect and the conclusions inferential. BENNETT girdled raspberry plants by removing a ring of bark and found that virus did not cross the girdle in either direction, from which he concluded (1927) that virus movement was in the channels through which elaborated food materials travel. CALDWELL concluded (1931) that normally the virus did not enter the water stream of plants, but, if introduced

experimentally, it might travel in the xylem vessels, though it did not pass into the phloem or other living cells unless the vessels were mechanically injured.

Virus pathologists usually describe the macroscopic rather than the histological or cytological features associated with the disease, consequently, little information has been recorded which portrays the cellular pathology of virus diseases.

The investigation of the histo-pathology of a virus disease was initiated (1913) by QUANJER when he discovered the relationship between phloem necrosis and the heavy accumulation of starch in the potato leaf affected with leaf roll. CARSNER and STAHL demonstrated (1924) necrosis of the phloem elements in sugar beets affected with the curly top disease, and subsequently Miss ESAU described (1933 and 1935) the complex series of necrosis and growth responses in the phloem degeneration of sugar beets affected with the curly top disease. The initial hypertrophy and hyperplasia of certain phloem cells resulted in the collapse and necrosis of the tissues. A second series of hypertrophic and hyperplastic changes occurred around the necrotic areas, resembling wound repair responses which led to the closure of internal cavities. Hypertrophy and hyperplasia outside the phloem produced protuberances on the veins of affected leaves.

DUFRÉNOY (1928) and SHEFFIELD (1933) have examined the cells of virus-affected leaves, showing that the formation of chlorophyll in them is characteristically inhibited and that they often have symptoms of hyperplasia. They concluded that chloroplast deficiencies were due to the inhibition of formation rather than to a destruction of plastids. DUFRÉNOY has also described the abnormal starch content or the fatty degeneration often occurring in the plastids of affected cells. Miss CLINCH discovered (1931) an enhanced formation of starch in the leaf-roll disease of potato plants. BAWDEN reported (1932) that necrosis in the leaf-roll disease of the potato remained localized in the phloem and, though accompanied by some enlargement of the adjacent parenchyma cells, did not result in cork formation.

Other and more profound physiological derangements of the host cells which may not appear until a comparatively late stage of a virus disease await elucidation.

Investigators soon found that virus disease symptoms are often modified, if not eliminated, by environmental conditions. JOHNSON reported (1922) that the optimum temperature for potato mosaic lay between 14-18°C., and that temperatures of 24-25°C. caused symptoms to disappear in one to two weeks. TOMPKINS reported (1926) that recovery from potato mosaic followed exposure of the infected plants for nine hours to temperatures above 24°C., although subsequently exposed to temperatures favorable to the virus. KUNKEL demonstrated (1934) that peach yellows and peach rosette in nursery trees were cured apparently by destruction of the virus, when they were exposed to temperatures of 34.4 to 36.3°C. for two weeks or longer. SPENCER found (1934) that nutritive conditions appreciably influenced the susceptibility of seedlings to yellow tobacco mosaic.

Our knowledge of the nature of the virus is still extremely hazy owing largely to the difficulty of obtaining it in pure state. The problem is complicated by certain unique difficulties, such as the

simultaneous existence of more than one virus in an affected plant, and the fact that in some plants an infectious virus may show no symptoms. BENNETT in 1932 concluded that insufficient information was available to indicate the number of distinct viruses involved in raspberry mosaic. Other investigators confirm the idea that diseases in plants due to composite viruses are not rare. K. M. SMITH demonstrated (1931) the composite nature of several potato mosaic diseases and succeeded in isolating at least two components which he designated X and Y.

The first definite proof of the agency of insects in transmitting virus diseases was obtained (1901) in Japan by TAKAMI, who succeeded in infecting healthy rice plants with the stunt disease, by means of a leaf-hopper (*Nephotettix*). Abundant evidence has since been obtained of the role of insects in virus transmission. Sucking, and, to a less extent, biting insects are capable of carrying the virus from plant to plant. BALL found (1906 and 1909) that curly top of the beet and other plants was carried by a leaf-hopper (*Eutettix*), and CARSNER and STAHL demonstrated (1924) that under field conditions the disease cannot be transmitted by any other agent. SEVERIN concluded (1923) that infected beet leaf-hoppers retain the infective principle of the curly top virus during life. KUNKEL found (1926) that aster yellows is transmitted by a leaf-hopper (*Cicadula*) and that a period of at least ten days' incubation of the juice of diseased plants in the leaf-hopper must elapse before the insect can infect healthy asters.

The voluminous literature on the subject of virus vectors contains many other discoveries, but lack of space forbids their discussion in this place. It seems advisable, however, to mention the selective transmission of plant viruses by insects and also the phenomenon of virus selection by the host plant. HOGGAN (1929) and K. M. SMITH (1929) showed that insects which had fed on tobacco plants containing more than one virus would transmit only one to a healthy plant. SMITH also showed (1931) that aphis transmission from a plant containing a complex of viruses would transmit only one disease, whereas needle inoculation transmitted a distinctly different virus.

Data on the power of the plant to select a certain virus from a complex are scanty. K. M. SMITH reported (1929) that aphids allowed to feed on potato plants affected with leaf roll and mosaic virus Y and subsequently colonized, some on potato and some on tobacco, transmitted leaf-roll only to the potato and mosaic only to the tobacco. Apparently the aphids acquired both viruses, but the plants selected one or the other from the complex.

BEIJERINCK's theory that the virus was a living contagium aroused no little comment and speculation in subsequent years. Various ideas were advanced by others. Attempting to explain the destruction of chlorophyll in the affected leaves, WOODS proposed (1899 and later) that the cause of the mosaic disease of tobacco might be an oxidizing enzyme. The hypothesis, accepted for a time, was later rejected, especially when it was found that some viruses do not destroy chlorophyll. Moreover ALLARD demonstrated (1916) that the oxidase of sap pressed from diseased leaves was destroyed by hydrogen peroxide without destroying the infectivity of the sap and, conversely, that infectivity may not be destroyed by treatments which impaired the oxidase.

IWANOWSKI made a cytological study (1903) of affected tissues and described plastic, ameboid bodies in the cells of diseased tobacco plants. Since the causal agent was filtrable, he concluded that these bodies must be the result rather than the cause of the disease. Subsequently other investigators described abnormal inclusions which they regarded as flagellates or protozoa and gave them various interpretations. Eventually, however, they were found to be inanimate bodies, products of the reaction of the cell to the presence of the virus. Miss GOLDSTEIN designated (1924) these enigmatical objects as X-bodies and KLEBAHN also studied them. The bodies are usually well-defined and stain more or less readily with aniline dyes. They vary in shape, are often rounded, and are typically vacuolated. KUNKEL (1921) found them in the Fiji disease of maize and NARASIMHAN (1928) in the Spike disease of sandal. J. HENDERSON SMITH was able to follow their development from the first to the final stages and emphasized (1930) that the X-bodies are not artefacts, nor degenerate forms of any of the organized structures of the cell. The evidence, pro and con, has been summarized by K. M. SMITH (1934) who shows that the weight of evidence supports the idea that X-bodies are reaction products rather than living, ameboid organisms.

DUFRÉNOY made comprehensive studies (1928 and 1935) on virus-affected cells. As stated in Chapter XI of this work, he described the phenomena of vacuolization in the course of which strands of cytoplasm penetrate all parts of the cell. These strands, he stated, contain many mitochondria, which may be short near the rounded vacuole, but otherwise long and filamentous with ends of adjacent elements apparently united. The mitochondria appeared to divide rapidly and, in leaves infected while young, evolved into amyloplasts — seldom into chloroplasts. The cytoplasm of virus infected cells lost its original physico-chemical properties and contracted into a vacuolated mass which was connected by many filaments with the cellulose wall at the points of intercellular communication. The X-bodies, DUFRÉNOY concluded, are merely portions of the chromatophilic cytoplasm which evolved into vacuolated masses. Another type of inclusion in virus-affected cells is the "striate material", discovered by RAWLINS and JOHNSON in 1925, which is usually found in contact with the nucleus, and may be related to it. This striate material may be seen in living cells, but the striations are accentuated by fixing agents.

Precise information about the nature of the ultimate virus particle was sought for many years. For a time the problem remained where IWANOWSKI left it when he showed that the virus passed through bacterial-proof filter tubes. DUGGAR and KARRER discovered (1921) that collodion filters were better than the porous clay cylinders originally used and concluded that the particle of the virus of tobacco mosaic was comparable in size to haemoglobin molecules, *i.e.*, $30\mu\mu$ in diameter, but subsequent workers did not agree on that point. THORNBERRY, who employed ultrafiltration methods, found (1935) that tobacco mosaic virus in purified preparations contained particles estimated to be $18\text{-}38\mu\mu$ in diameter.

The problem of the actual nature of the virus particle was evidently outside the field of conventional biological investigations. Opinion was divided for some time as to whether the virus particle was a submicroscopic organism or some new type of infectious

agent. Those who held the former idea were inclined to follow IWANOWSKI, those who held the latter followed BEIJERINCK. The evidence initially obtained did not unqualifiedly support either opinion.

VINSON and PETRE successfully separated (1927 and later) the virus tobacco mosaic from much of the extraneous material, precipitated and redissolved it. They found two fractions which could be separated by heat-precipitation, one at about 85°C., and another above 90°C. After the removal of the first fraction, which contained an appreciable amount of nitrogen, the plant juice was still infectious, although the concentration of the virus was appreciably reduced. TAKAHASHI and RAWLINS discovered (1933) the property of stream double refraction when the sap of mosaic tobacco plants was examined in polarized light. The phenomenon was interpreted to mean that the virus of tobacco mosaic, or some substance regularly associated with it, is composed of submicroscopic rod-shaped particles, possibly liquid crystals or tactoids.

The results of a vast amount of work on virus afforded evidence, confusing at times, of its protein nature, but without definite proof that it was an organized protein, one great obstacle being the difficulty of obtaining the virus in a pure state. When STANLEY prepared (1935 and 1937) from mosaic-affected plants a crystalline protein which had all the properties of a virus, a technique for further studies was available. He found that from 80 to 90 percent of the total protein of severely affected tobacco plants might consist of this virus protein, and that this material was about 500 times more infective than the original. One cc. of a solution containing 10^{-9} grams per cc. of the protein usually proved infectious to plants. WYCKOFF, BISCOE, and STANLEY determined (1937) that the protein had a molecular weight of 17,000,000. The conventional tests indicated that the crystals were protein and that infectivity was lost if the proteins were denatured by heat. They were not digested by trypsin, but were digested slowly by pepsin with loss of infectivity. Tomato leaves which had been infected with the tobacco mosaic virus yielded the same protein as STANLEY had obtained from affected tobacco plants, but none was obtained from healthy tobacco and tomato plants. BAWDEN also isolated (1936) nucleoproteins from sap of virus-affected plants and concluded that each nucleoprotein molecule has a semiregular structure, being built of approximately similar subunits. LORING and STANLEY isolated (1937) four distinctly different crystalline high molecular-weight proteins from the four different strains of tobacco mosaic designated as "ordinary", "single lesion", "yellow", and "masked". STANLEY concluded that the mutation which originates a new strain of virus is accompanied by the production of a new protein.

In view of the specific dysgenic activity of these protein molecules when they enter the living cell and of their ability to incite the production of more molecules of their kind, some revision of the conventional ideas of living matter has been suggested. The situation recalls the startling inovations introduced during the previous century by the proponents of the cell theory and by the pathologists. STANLEY proposed (1937) that this type of protein molecules may be considered as infectious agents in the same

category as bacteria, fungi, and protozoa. The entrance of a few molecules of a virus protein into the cells of a susceptible host plant may alter the processes of metabolism to such an extent that they produce, not normal protein, but great quantities of virus protein. The resulting changes in the metabolic equilibrium of the cell constitute what we call disease.

It is obviously premature to formulate a satisfactory and comprehensive idea of the nature of virus diseases, since the problem is still in the stage of discovery and exploration. The casual agent is so different from any heretofore associated with diseases of plants that it is imperfectly envisioned. In a field where so much dogmatism and hasty observation have occurred, it is natural that investigators did not see eye to eye.

Resistance to virus diseases in the plant kingdom appears to be widespread, with the exception of the families *Solanaceae, Leguminosae,* and *Rosaceae.* Investigations have shown that in each susceptible species or variety there may be strains which have sufficient resistance to be valuable for cultivation.

In 1933 a new strain of sugar beets showing remarkable resistance to the curly top disease was isolated and described by CARSNER and his colleagues. This strain, designated U. S. No. 1, possesses such resistance that it has become a commercially important variety. ABEGG and OWEN discovered (1935) that resistance to the curly top disease of beets is conditioned by a partially dominant factor C, which is linked to the red-crown factor R with 20-30 per cent crossing over. The factor C has been found associated with selections from the resistant variety designated U. S. No. 1. PIERCE and WALKER developed a mosaic resistant Refugee bean from a single plant selected in 1929. When crossed with Refugee green, it gave completely resistant hybrids which segregated in the F_2 generation for resistance and susceptibility. Ultimately resistant families were isolated. It was uncertain whether the inheritance was strictly Mendelian.

The probability that one virus may immunize the host plant against another was suggested by THUNG (1931), SALAMAN (1933), KUNKEL (1934), PRICE (1934), and K. M. SMITH (1935). The immunity was conferred, however, only by similar viruses and virus strains, not by a virus of a different type. For example, when a healthy tobacco plant and one infected with the green strain of tobacco mosaic are infected with the yellow strain, the healthy plant only develops the characteristic yellow spots. SPENCER demonstrated (1935) that the state of nutrition influenced the susceptibility to tobacco mosaic virus. The application of small amounts of potassium increased, but larger amounts decreased the susceptibility of the plants.

Agriculturists and experimenters have long had a vague notion of dysgenic factors which caused some clons to "run out" while others retained their virility and integrity. It is now experimentally demonstrated that deterioration was due in most cases to infection with virus diseases not originally recognized. The stability of clons may well be related to their resistance to virus infection, whether due to genetic immunity or to characters which repel virus-carrying insects. The problem awaits comprehensive investigation.

The control of plant diseases:- The quest for prophylactic measures is almost invariably the goal of researches on the etiology of plant diseases. The prodigious economic losses frequently encountered in modern agricultural operations have impelled specialists to undertake new and highly technical investigations. The continually increasing growth of knowledge has changed the many popular ideas of plant disease. Not many generations ago our ancestors believed implicitly in witchcraft, sorcery, and magic. As long as blights and mildews of crop plants were assumed to be due to mystical causes, it is small wonder that people resorted to preventive measures of a superstitious nature, such as incantations, sowing seed in the dark of the moon, and sticking branches of laurel trees in the grain-fields to absorb the "blighting vapors". It was many years before scientifically directed measures were practiced. The pioneer work of men like PRÉVOST, ROBERTSON, and KNIGHT seemed as good as lost. In the course of time, however, scientific investigators found methods for partly controlling some of the most destructive diseases and thus opened the way for further discoveries.

The inception of the modern period of plant disease control was due to a discovery in France in 1882, made by MILLARDET whose investigations on the vine mildew have been mentioned. It is sometimes said that his discovery of the efficacy of copper sulfate-lime mixtures as fungicides was purely fortuitous, but the following quotations indicate that quite the contrary was the case. His account of the discovery was prefaced by the following:

"Since the appearance of mildew in France in 1878, I have not ceased to study *Peronospora* in the hope of discovering in its development some vulnerable point that might permit of its mastery. The results of my observations are set forth in various publications.

"I had noticed in the course of my researches that the summer spores or conidia of *Peronospora* easily lose their germinating power. This observation and the failure of all the treatments attempted until then had led me to formulate this conclusion, - that a practical treatment of mildew ought to have for its objective not the killing of the parasite in the leaves infected by it, which seems impossible without killing the leaves themselves, but of preventing its development by covering, preventively, the surface of the leaves with various substances capable of making the spores lose their vitality or, at least, of impeding their germination". (From translation by F. J. SCHNEIDERHAN, 1933).

MILLARDET had observed that the conidia did not germinate in water from his domestic well, though he did not ascertain until later that it was due to the presence of a small amount of copper derived from the brass pump. When, however, he observed (1882) that vine leaves sprinkled with a lime and copper sulfate spray to discourage thievery were free from mildew, he started to investigate anew the action of copper salts on the conidia of mildew.

Spraying experiments conducted during the next two years in the Médoc and in Central France gave proof that covering leaves and young buds of the vine with Bordeaux mixture before they were infected with spores of the *Plasmopara* protected the crop, whereas unsprayed vines would develop rot on the infected bunches, would suffer defoliation, and produce no crop (Fig. 37). The idea of preventive treatment is so familiar to us now that it is hard to realize that it seemed so preposterous to men of that time.

MILLARDET published his results in 1885, and stated in conclusion

"All of these considerations, it seems to me, sufficiently warrant my affirming in the most positive manner the efficacy of the treatment, concerning which I speak, against a scourge that, until now, has withstood all efforts in Europe as well as in America; that is to say, mildew, properly speaking, and rot or mildew of grapes. But there is more; the close analogies that exist between the *Peronospora* of the vines and that causing the disease of the potato and tomato cause me to hope that we shall henceforth have at hand a real prophylactic treatment for these latter diseases". (From translation by F. J. SCHNEIDERHAN, 1933).

MILLARDET gave directions for preparing the fungicide by mixing lime water (freshly prepared) and copper sulfate solution and emphasized the necessity of its application prior to fungus infection. This fungicide which has since been known as "Bordeaux mixture" was promptly tested in England and America and found wide application in many other countries. The successful combination of Bordeaux mixture with arsenical compounds for the control of insects increased its value. So far as known, MILLARDET made no effort to obtain pecuniary gains from his discovery.

Lime-sulfur solution, consisting of a mixture of calcium polysulfides, was employed in France as early as 1852, but apparently did not come into general use as a fungicide at that time. M. GRISON, chief gardener of the plant houses at Versailles, appears to have been the first to employ heat in the preparation of this fungicide. Lime-sulfur solution was used at that time for the control of *Oidium Tuckeri* on grape vines and was applied with the type of pump-syringe at that time commonly used in glass house work. In deference to the man who made the discovery, the method was called, at the time, "Procédé Grison".

The use of lime-sulphur solution in American orchards appears to have been started about 1880 in California. A combination of lime, sulfur and salt had been used in Australia as a sheep dip for scab, and later for the same purpose in California. The spray was in general use on peach trees in and about Hanford and Visalia, California, as early as 1883, 1884, and 1885. The concentrations then employed were suitable only for application during the season in which the trees were dormant, but it was soon found to be efficacious for the control of peach leaf curl. NEWTON B. PIERCE (1900) made an extensive report on the treatment of trees and gave publicity to the use of lime-sulfur solution as a dormant spray. A dilute lime-sulfur solution eventually proved valuable as a summer spray on fruits which would be injured by copper-containing solutions. CORDLEY of Oregon and PIPER of Washington elaborated (1906-1908) this technique which rapidly was adopted in many regions.

Long years after PRÉVOST's attempts to kill bunt spores on seeds the problem of seed disinfection was again taken up. JENSEN described (1888) a method for treating oat seed to kill adhering Ustilago spores by a modified hot water treatment, subsequently employed with great success. The use of formaldehyde for seed disinfection was announced in 1888 by TRILLAT in France and in 1895 by GENTHER in Germany. BOLLEY demonstrated (1897) its usefulness as a germicide for seed-borne diseases of flax in North Dakota. Formaldehyde has long been utilized for treating seed potatoes to prevent scab. Formaldehyde dust was prepared in

1926 by SAYRE and THOMAS for the control of oat and onion smuts and to prevent the damping-off of seedlings. This dust was prepared by mixing commercial formalin with infusorial earth or other inert absorbents. DARNELL-SMITH's work in Australia demonstrated (1915) that dry, finely ground copper carbonate is an effective fungicide for the bunt of wheat and since that time dusting of seed has been increasingly employed. Organic compounds of mercury were introduced in 1912 in Germany as seed disinfectants and found to be effective for the control of cereal diseases. A chlorophenol mercury compound was placed on the market about 1915 in Germany under the trade name of "Uspulun". Subsequently similar compounds designated "Chlorophol" and "Semesan" were placed on the market in the United States. In general it may be said that organic mercury seed-disinfectants produce very little injury to the seed so treated.

Investigators at Cornell University and elsewhere perfected the art of making and applying sulfur dusts for the control of fungi on fruit and vegetable crops, reviving, as it were, the classical discoveries of ROBERTSON and others. Finely-divided sulfur has been produced through new and effective processes of grinding, which is an excellent product for spraying and dusting purposes. Organic compounds of sulfur, such as dithiocarbonic acid, have given promising results. Bordeaux mixture, also, has been prepared as a powder, mixed with suitable inert materials and applied economically as a dust. Some of the so-called insoluble coppers have been used successfully on Bordeaux-sensitive plants and on crops used for canning, *e.g.*, tomatoes. Efficient machines for blowing these dusts on plants have been in general use for several years. In some cases the work of dusting has been successfully and economically done by the use of airplanes.

For long years farmers have practiced an empirical selection of disease resistant varieties. No individual can claim the sole credit for the control of plant disease by the introduction of immune or resistant crop plants. The pioneer work of men like BOLLEY and ORTON was successfully continued by BAIN, ESSARY, FREEMAN, JOHNSON, JONES, NORTON and others. The survival of a system of agriculture has often depended chiefly on the resistance of the crop plants to disease. In the agro-biological province disease is as much a part of the environment as drought, cold, or heat. The control of plant diseases by fungicides must be regarded as a technique which should be abandoned eventually when resistant plants shall have been introduced.

Modern agricultural explorations have paid great attention to varieties which possess notable resistance to disease. Happily some degree of success has been achieved in introducing into cultivation some of these races. The use of resistant stocks in the propagation of fruit trees has been extensively employed in the last half century. A recital of the work cannot be attempted in this place.

Recognition of the inherent resistance of native or introduced crop plants to diseases encouraged attempts to hybridize them with cultivated races. Since the opening years of the 20th century this work has progressed. It was logical to start the breeding of varieties resistant to pathogens like *Fusarium* which inhabit the soil and penetrate the roots of plants. The success attending the initial work of ORTON with cotton, cowpeas, and watermelon in the United

States encouraged others to attack the problem. Through a period of thirty years the United States Department of Agriculture in coöperation with state experiment stations and with institutions in Canada has been developing rust-resistant varieties of wheat. The hybrid varieties which have been obtained possess resistance to rust and yield flour having excellent milling and baking qualities. Numerous examples have been cited previously in this chapter. Breeding resistant plants has become increasingly important since the discovery of virus diseases for which the ordinary application of germicides is obviously useless.

Definite progress is being made in the genetics of plant disease resistance. In the case of a few crops like sugar cane and sugar beets the results are rather spectacular. COONS (1936) estimated that on nearly 1/4 the total farm acreage of the United States varieties recognized as disease resistant were planted. The Extension Service of the Department of Agriculture of the United States listed 14 important vegetables, of which there were 123 varieties known to possess resistance to diseases of various kinds.

HARTLEY and RATHBUN-GRAVATT pointed out (1937) that the effect of Phytophthora on potatoes increased the variability of the national yields, as illustrated by the tragic effects of the crop failure resulting in the historic Irish famine of 1845. They also gave credit to the progress which has been made in the control of this disease as a stabilizing factor in agriculture. The control has changed it from a catastrophic thing that upset all expectations into one that no longer seriously affects the dependability of total regional yields.

Governmental inspection of plants or of fruits for the purpose of eliminating infected material is a comparatively recent phase of plant disease control. In several European and American countries there is inspection at ports of entry whereby plants bearing evidence of certain diseases are prohibited entry. Phytopathologists and entomologists generally coöperate in the work of inspection. The inspection of plants and control of shipments was undertaken by various countries after it became evident that some serious epidemics had been inadvertently introduced and, free from their natural checks, often spread with unwonted rapidity.

The problems of control are thus briefly enumerated and it will be evident that they are relatively new. Further work is needed to bring greater precision into the field. Closer coöperation between pathologists, physiologists, and biochemists is needed to solve the more elusive phases of the problems. An international arrangement for the control of plant diseases is most urgently needed, since it is known that international boundaries are no barrier to them.

A retrospective glance at the history of plant pathology reveals some efforts to bring many diverse factors into operation in the control of plant diseases. The zealous amateurs and experienced farmers had such inadequate technique that they made little progress until their problems were clarified by mycologists in the middle of the 19th century. The enlightening results of DE BARY's experiments with pure cultures of fungi, his concepts of parasitism, and the etiology of disease were as life-giving waters in the desert.

In the closing years of the 19th century valuable information concerning the life histories of pathogenic fungi began to be ob-

tained by scientifically trained men who took their work to the field. Consciously or unconsciously they evolved a new technique in the study of the etiology of plant diseases. These men found problems which could not be solved in the fusty cabinet, nor within the limits of the laboratory. Out in the open air they began to understand the epidemiology of diseases and there to see how many hitherto unsuspected phenomena had been overlooked. They were a new generation of plant pathologists many of whom were deeply impressed by the tragic results of crop losses caused by plant diseases.

The field pathologists often obtained valuable clues from the farmers, and, in turn, taught them what had been learned by scientific research. In field-meetings, in farmer's associations, and in agricultural societies, many thousands received instruction in the life history of pathogenic organisms and in the principles of disease control.

It is true that hasty surveys of doubtful value were sometimes made, but discoveries of alternate hosts, of resting stages, of infective centers, of air-borne spores followed the work of the field investigators. A wealth of specimens on which further investigations were made came to the laboratories and herbaria. The field pathologists came to know the place of fungi in the complex living world and to extend the discoveries of the laboratory. It was like the great period of expansion which followed the 18th century botanical explorations in the Antipodes, the Indies, and in the New World.

Among many who originally worked in what may be termed agropathology, one may mention the following: HARTIG and ADERHOLD in Germany; PRILLIEUX, DELACROIX, and VIALA in France; WARD and SALMON in England; ERIKSSON in Sweden; BURRILL, HALSTED, BESSEY, NEWTON B. PIERCE, and STEWART in the United States.

While the investigation of the diseases caused by fungi was rapidly advancing, the field was extended by the discovery of a small, but important group of diseases caused by bacteria and with it an appreciation of the rôle of insects in disseminating the pathogenic organisms.

The diseases caused by viruses had long eluded scientific researches although their existence had impressed itself on the agricultural world for many generations. BEIJERINCK's work in the closing years of the 19th century placed the virus problem clearly before the scientific plant pathologists. Knowledge of this obscure etiological agent has grown in the last 20 years and has elucidated many fundamental problems in plant pathology.

From year to year plant pathology has invoked the assistance of cognate branches of science such as physiology, genetics, chemistry, physics, and meteorology. Its recognition was earned through demonstrations of its significance in agriculture, forestry, and to a certain extent, in medicine. The establishment of departments of plant pathology in universities and in governmental agencies has occurred within the memory of many now living.

The international aspects of pathology have been the subject of comment. Plant diseases are not merely national problems. Students who have been eager to avail themselves of the oppor-

tunity to study in foreign countries have found hospitable welcome in the important centers of research of all nations.

The discoverers have made no attempts to enrich themselves at the expense of those who benefitted by the discoveries.

Finally, the control measures evolved have been given the widest publicity for the stabilization of the agricultural industries and for the increase of the world's food supply.

REFERENCES

APPEL, O. (1915): Disease resistance in plants. Science, 41: 773-782.

ARTHUR, J. C. (1929): The plant rusts (Uredinales). Wiley, New York; Chapman & Hall, London.

BAWDEN, F. C. (1939): Plant viruses and virus diseases. Chronica Botanica, Waltham, Mass. (formerly Leiden).

BUTLER, E. J. (1936): The nature of immunity from diseases in plants. 3rd. Internat. Congress of Comp. Pathol., 1(2):1-14.

DELACROIX, G. (1908-09): Maladies des plantes cultivées. Baillière, Paris. (Tome 2 by GEORGES DELACROIX and ANDRÉ MAUBLANC).

DUFRÉNOY, J. (1935): Structure et Métabolisme cellulaires. Arch. Anat. Microscop. 31: 5-77.

ERIKSSON, J. (1930): Fungous diseases of plants in agriculture, horticulture and forestry. 2d ed., tr. from the German by W. GOODWIN. Baillière, Tindall and Cox, London.

HARTIG, R. (1900): Lehrbuch der Pflanzenkrankheiten. 3. völlig neubearb. Aufl. des Lehrbuches der Baumkrankheiten. Springer, Berlin.

———— (1894): Text-book of the diseases of trees. Transl. by W. SOMERVILLE, Rev. and ed. by H. M. WARD. Macmillan, London and New York.

HEALD, F. D. (1933): Manual of plant diseases. 2d ed., McGraw-Hill, New York and London.

HUMPHREY, H. B. (1936): The development of disease resistant plants. 3rd. Internat. Congress of Comp. Pathol., 1(2):267-274.

PIERCE, N. B. (1892): The California Vine Disease. U. S. Dept. Agr., Div. Veg. Path., Bull. 2.

PRÉVOST, B. (1807): Mémoire sur la cause immédiate de la carie ou charbon des blés. Bernard, Paris. English transl. by G. W. KEITT, 1939, Phytopath. Classics no. 6.

PRILLIEUX, E. (1895-97): Maladies des plantes agricoles. Firmin-Didot, Paris.

REESS, M. (1888): ANTON DE BARY (biography). Ber. D. Bot. Gesellsch. 6: VIII-XXXI.

SMITH, E. F. (1905-14): Bacteria in relation to plant diseases. Carnegie Inst. of Washington, Pub. no. 27, v. 1-3.

SMITH, K. M. (1933): Recent advances in the study of plant viruses. Churchill, London. (Contains valuable bibliography).

SORAUER, P. (1933): Handbuch der Pflanzenkrankheiten. 6. neubearb. Aufl., hrsg. von Dr. O. APPEL. Parey, Berlin.

STANLEY, W. M. (1937): Crystalline tobacco-mosaic virus protein. Amer. Jour. Bot. 24: 59-68. (Contains valuable bibliography).

TILLET, MATHIEU DU (1755): Dissertation sur la cause qui corrompt et noircit les grains du bled . . . . Brun, Bordeaux. English transl. by HUMPHREY, 1937, Phytopath. Classics no. 5. Ithaca, N. Y.

WHETZEL, H. H. (1918): An outline of the history of phytopathology. Saunders, Philadelphia. (With bibliography).

WORONIN, M. S. (1878): Plasmodiophora brassicae, Urheber der Kohlpflanzen-Hernie. Jahrb. wiss. Bot. 11: 548-574. English transl. by C. CHUPP, 1934, Phytopath. Classics no. 4.

Chapter XX.

SIGNIFICANT NAMES IN THE HISTORY OF BOTANY.

The young student often becomes bewildered by the vast number of names of workers in his chosen field of study. Although there is no precise means for estimating the renown of great men, each student of their works tries to formulate an approximate estimate of their importance. After consideration of the matter, and in consultation with various colleagues, I have drawn up the following list of 50 important names in the hope that it may stimulate others to make similar attempts. To facilitate the estimation of their eminence, four groups have been made concerning which I beg to offer the following explanation:

1. Discoverers: men who may be considered notable because of the basic botanical knowledge which they discovered.
2. Describers and Classifiers: men who made successful attempts to systematize the knowledge of the plant kingdom.
3. Specialists: men who made important discoveries in certain fields. (The distinction between this class and the Discoverers is not sharply defined).
4. Exponents: men who by the excellence of their skill in teaching or writing have made significant contributions to the literature of botany.

It is evident that a few names are included in more than one category.

Discoverers	*Describers and Classifiers*	*Specialists*	*Exponents*
GREW (1628-1711)	THEOPHRASTUS (371-286 B.C.)	INGEN-HOUSZ (1730-1799)	DIOSCORIDES (First century A. D.)
MALPIGHI (1628-1694)	BAUHIN (1511-1582)	FRIES (1794-1878)	GHINI (1490-1556)
CAMERARIUS (1665-1721)	JUNG (1587-1657)	DARWIN (1809-1882)	CORDUS (1515-1544)
HALES (1677-1761)	RAY (1628-1705)	TULASNE (1815-1885)	SENEBIER (1742-1809)
DE SAUSSURE (1767-1845)	DE JUSSIEU (1748-1836)	MENDEL (1820-1884)	VON HUMBOLDT (1769-1859)
VON MOHL (1805-1872)	LINNAEUS (1707-1778)	HOFMEISTER (1824-1877)	SCHLEIDEN (1804-1881)
VON NÄGELI (1817-1891)	PERSOON (1761-1836)	DE BARY (1831-1888)	DE CANDOLLE (1806-1893)
SACHS (1832-1897)	DE CANDOLLE (1806-1893)	BEIJERINCK (1851-1930)	GRAY (1810-1888)
PFEFFER (1845-1920)	J. D. HOOKER (1817-1911)	GOEBEL (1855-1932)	SACHS (1832-1897)
DE VRIES (1848-1935)	DE BARY (1831-1888)	WINOGRADSKI (1856-1934)	STRASBURGER (1844-1912)
			PFEFFER (1845-1920)

AUTHOR *and* SUBJECT INDEX

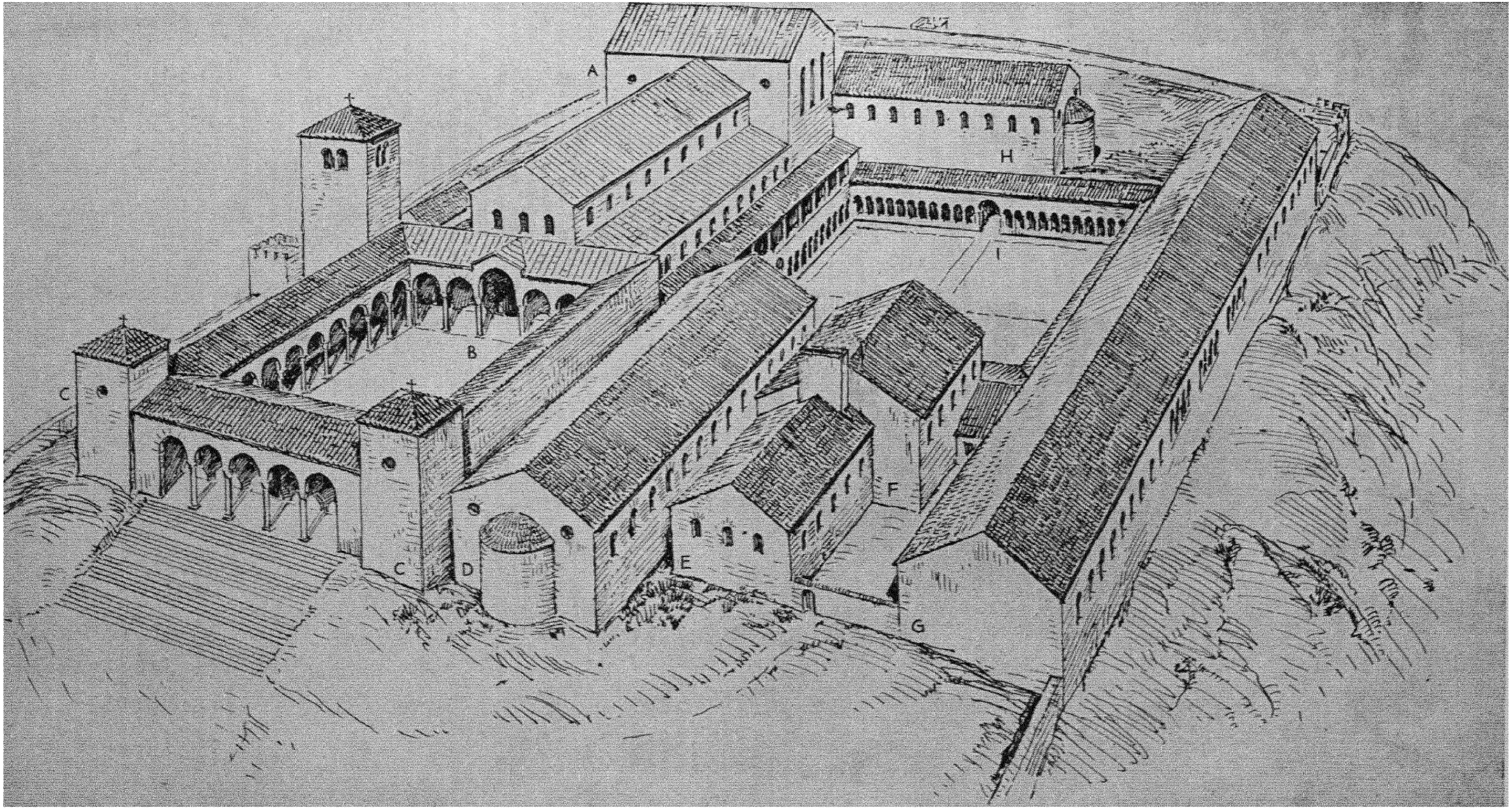


FIG. 28. — ***Monte Cassino*** in Campania, Italy, one of the oldest botanical centers in Europe. A repository for many classical manuscripts and a portal for the entry of Arabic learning into Europe. A reconstruction of the Abbey built by Desiderius (reigned 1058-1087) drawn by K. J. CONANT and reproduced by permission of *Speculum*. (Vide WILLARD, H. M., Plate 1, Speculum, Vol. 10, 1935).

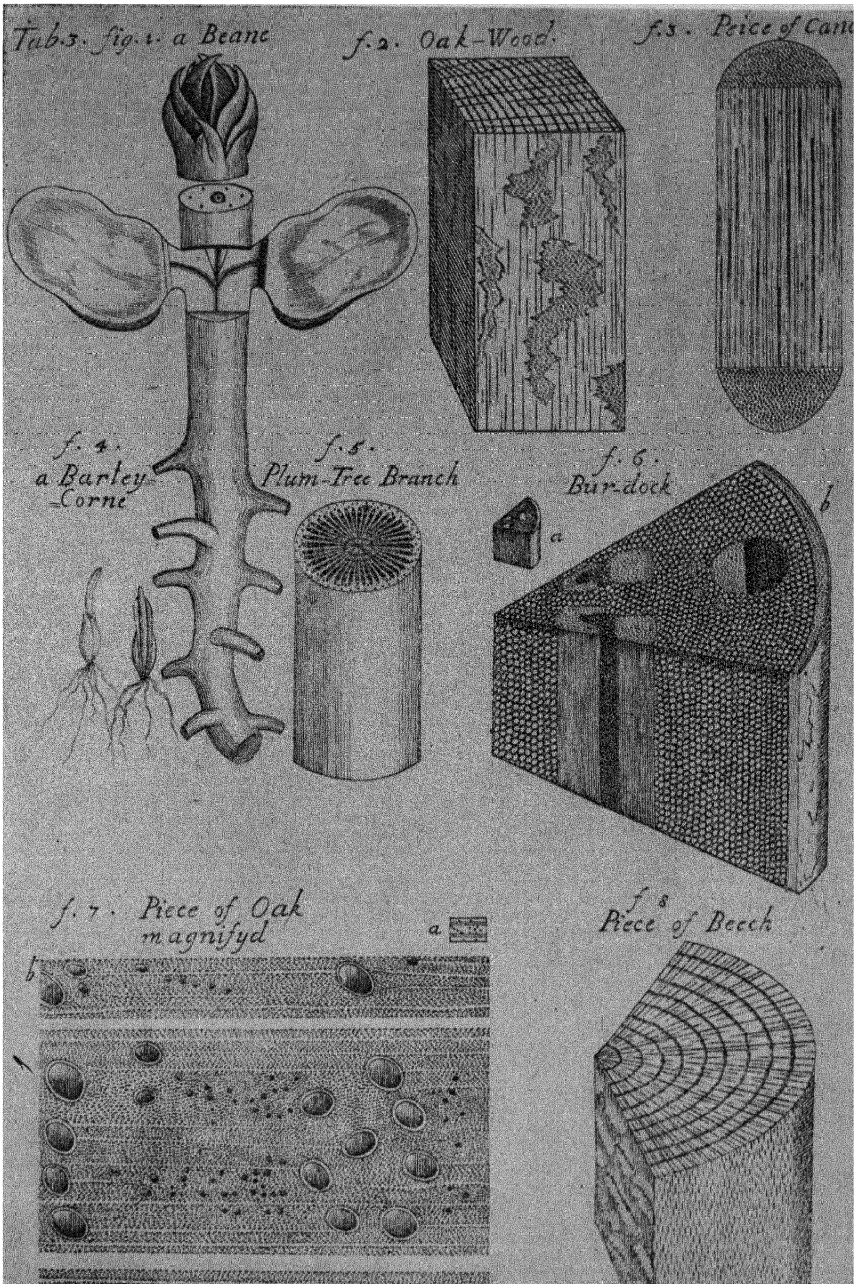


FIG. 29. — One of the tables from GREW's Anatomy of Plants, London 1682. F.1. The Bud cut transversly, and part of the Radicle by the Length, in a Bean newly sprung up. F.2. Sheweth the Wood as it appears to the naked Eye. F.3. the Cane split down. F.4, the Corn newly sprouted. F.5. A Branch of five years growth. From the Circumference, to the utmost black Ring, goes the Barque. F.6. a, a piece of the Stalk; b, magnified. F.7. a, a piece of Oak-wood cut transversly; b, the same magnified. The white Lines are the lesser and greater Insertions. The Pricks, are the Wood. The little and great Holes two sorts of Aer-Vessels. F.8. Part of a Branch ten years old, with the Barque stripped off, and cut both transversly and down the length, to shew how the Barque is inserted into the Wood.

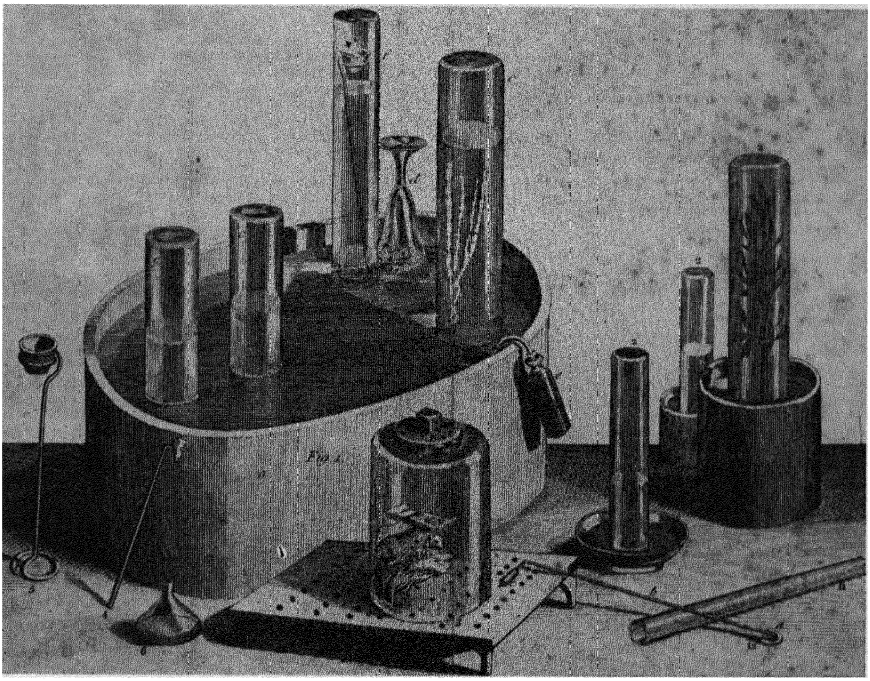


FIG. 30. — Apparatus used by JOSEPH PRIESTLEY to demonstrate the evolution of **oxygen.** Fig. 1, *a*, pneumatic trough; *b*, flat stones; *c*, cylindrical jars; *d*, tall beer glass inverted over a mouse; *e*, small bottle from which gases were introduced to cylinders. Fig. 2, cylindrical jars. Fig. 3, weighted receiver in which mice were kept. Fig. 4, angled rod bearing a conical cork. Fig. 5, support for a small dish ("gallipot"). Fig. 6, funnel. Figs. 7 to 10 not shown in this plate. Fig. 11, glass cylinder. Fig. 12, wax candle on an angled rod. — From "Experiments and Observations on Different Kinds of Air", Vol. I (Ed. 1790).

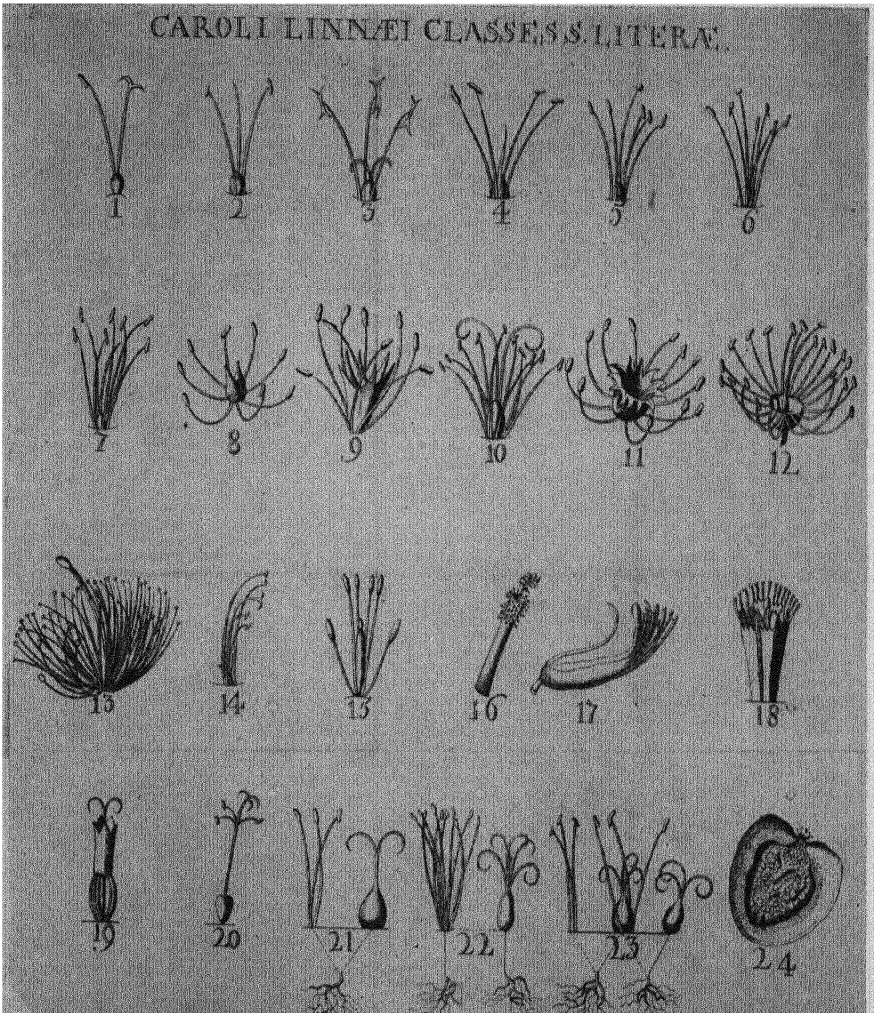


FIG. 31. — The Linnean classes of plants as shown in one of the plates of Genera Plantarum, Ed. 1, 1737. — 1, *Monandria;* 13, *Polyandria;* 14, *Didynamia;* 18, *Monadelphia;* 20, *Gynandria;* 21, *Monoecia;* 24, *Cryptogamia.*

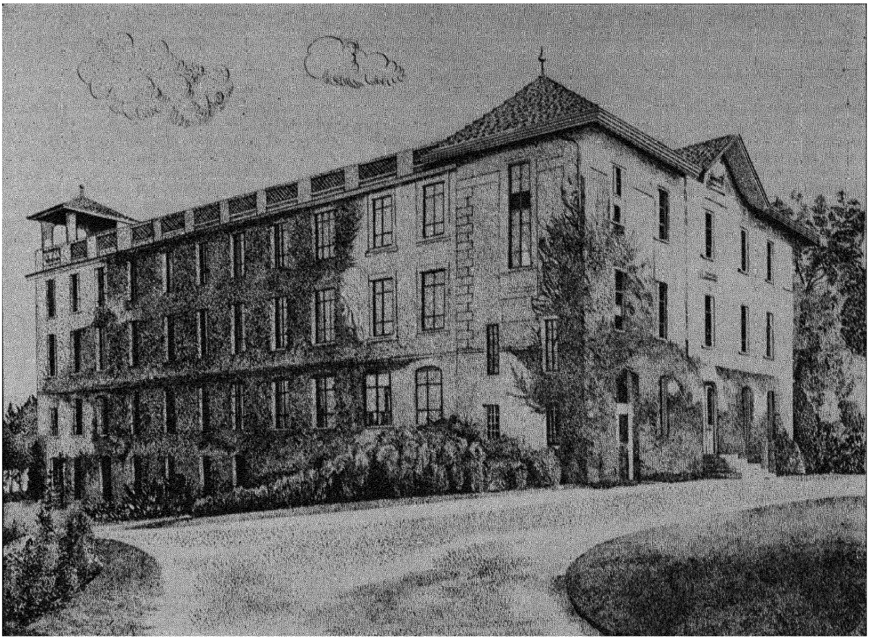


FIG. 32. — The Conservatoire Botanique at Geneva (drawn by C. C. TEBBUTT). The Conservatoire stands, near the buildings of the League of Nations, in the Botanical Garden, which was inaugurated by AUGUSTIN PYRAME DE CANDOLLE in 1817. He started building the Conservatoire about 1824. The Herbier DELESSERT was added in 1869 and the present building, shown above, was inaugurated in 1904 and enlarged in 1912.

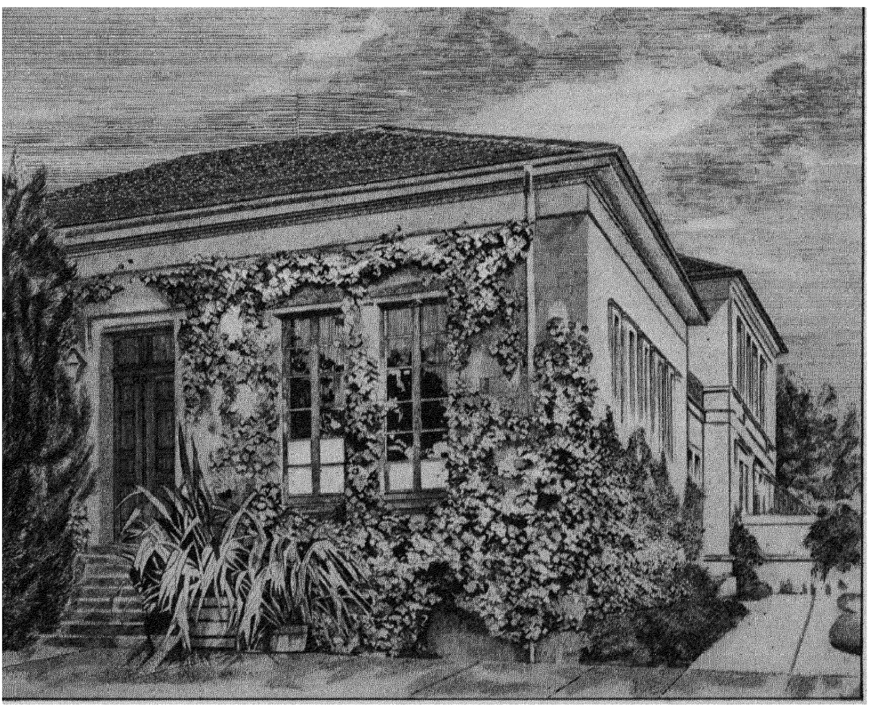


FIG. 33. — The Botanical Institute built by VON MOHL at the University of Tübingen, at which so much fruitful research work has been done. Drawn by C. C. TEBBUTT after a photograph by D. T. MACDOUGAL.

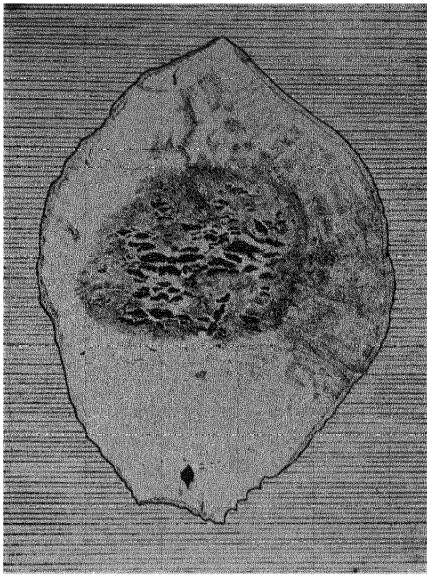


FIG. 34. — "Brown Heart" of turnips due to boron deficiency. The necrosis and cracking of the tissue in the turnip are symptoms of extreme deficiency. Reproduced by permission from HURST and MACLEOD, Sci. Agr. 17:209-214 (1936).

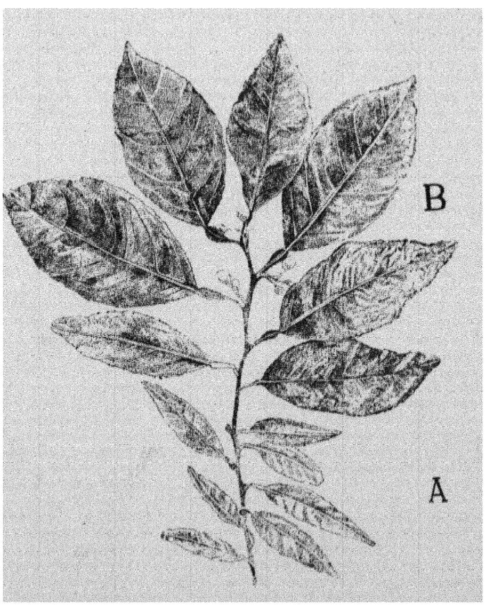


FIG. 35. — Orange twig showing the effect of zinc deficiency upon leaf and shoot growth. A, the portion of the twig which developed while zinc was deficient; B, portion which developed after the tree had been sprayed with a zinc-lime mixture. Drawn from an original photograph by the author.

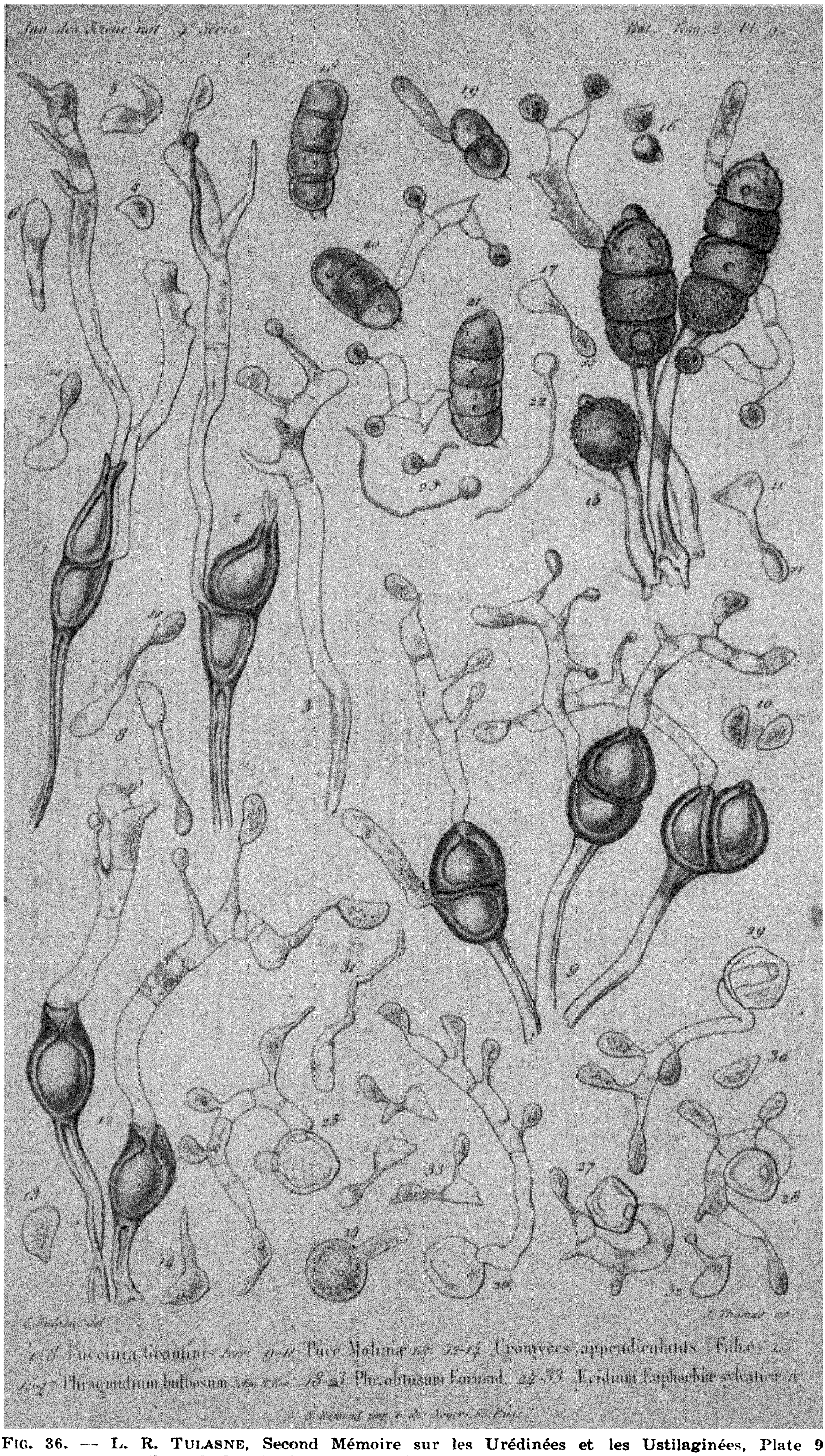


FIG. 36. — L. R. TULASNE, Second Mémoire sur les Urédinées et les Ustilaginées, Plate 9 (legend above), *from* Ann. Sci. Nat., Bot., Sér. 4 t. 2, 1854).

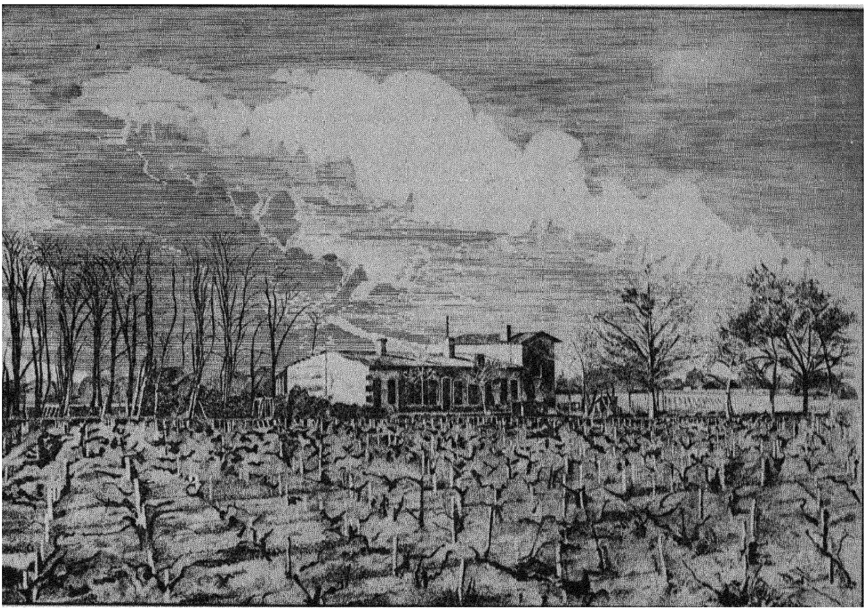


FIG. 37. — Farmhouse and Vineyard in the Medoc Region of France in which MILLARDET conducted his work on the use of copper sulphate and lime mixtures for the control of vine mildew. Drawn by C. C. TEBBUTT after a photograph by W. V. CRUESS.